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Fishery Bulletin

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Patterns of growth, mortality, and size of the tropical damselfish *Acanthochromis polyacanthus* across the continental shelf of the Great Barrier Reef

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Abstract—Age-based analyses were used to demonstrate consistent differences in growth between populations of *Acanthochromis polyacanthus* (Pomacentridae) collected at three distance strata across the continental shelf (inner, mid-, and outer shelf) of the central Great Barrier Reef (three reefs per distance stratum). Fish had significantly greater maximum lengths with increasing distance from shore, but fish from all distances reached approximately the same maximum age, indicating that growth is more rapid for fish found on outer-shelf reefs. Only one fish collected from inner-shelf reefs reached >100 mm SL, whereas 38–67% of fish collected from the outer shelf were >100 mm SL. The largest age class of adult-size fish collected from inner- and mid-shelf locations comprised 3–4 year-olds, but shifted to 2-year-olds on outer-shelf reefs. Mortality schedules (Z and S) were similar irrespective of shelf position (inner shelf: 0.51 and 60.0%; mid-shelf: 0.48 and 61.8%; outer shelf: 0.43 and 65.1%, respectively). Age validation of captive fish indicated that growth increments are deposited annually, between the end of winter and early spring. The observed cross-shelf patterns in adult sizes and growth were unlikely to be a result of genetic differences between sample populations because all fish collected showed the same color pattern. It is likely that cross-shelf variation in quality and quantity of food, as well as in turbidity, are factors that contribute to the observed patterns of growth. Similar patterns of cross-shelf mortality indicate that predation rates varied little across the shelf. Our study cautions against pooling demographic parameters on broad spatial scales without consideration of the potential for cross-shelf variability.

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Coral reefs are spatially diverse and heterogeneous marine environments. The Great Barrier Reef (GBR) is the largest reef system and represents a near-continuous matrix of over 2400 individual reefs spanning a distance of some 2000 km along the coast of Queensland, eastern Australia (Fig. 1). Coral reef habitats are subject to the influences of environmental (e.g., exposure and proximity to coastlines), as well as biotic processes (e.g., availability of food). Strong cross-shelf abiotic and biotic gradients (Wilkinson and Cheshire, 1988) have the potential to influence patterns of abundance and demographic characteristics of fishes associated with coral reefs. Several studies have examined the broad-scale abundance and distribution of a wide variety of organisms across the continental shelf of the GBR, including hard corals (Done, 1982), soft corals (Dinesen, 1983), crustaceans (Preston and Doherty, 1990, 1994), algae (McCook et al., 1997), and reef fishes (Williams, 1982, 1983; Williams and Hatcher, 1983; Russ, 1984a, 1984b; Newman and Williams, 1996; Newman et al., 1997; Gust et al., 2001, 2002). Great cross-shelf differences in abundance are common within and among taxa. Although environmental gradients have often been implicated as causing these patterns and it is also known that environmental features influence demographic characteristics (e.g., growth), there have been few comparisons of demographic characters by geography and spatial scale.

Demographic measures are crucial to understanding population dynamics. Population demographics of a number of many fish species have been shown to vary at spatial scales ranging from 100's of m to 100's of km (Gillanders, 1995; Meekan et al., 2001; Gust et al., 2002). With the exception of data on a few commercially important taxa (Munro and Williams, 1985; Williams et al., 2003) and some others (e.g., acanthurids and scarids; Choat and Axe, 1996), there are few data on demographic parameters of coral reef fishes and even less on spatial variation within these parameters. Variation in demographics may be common across the shelf. For example, significant differences in the size frequency, growth, mortality, and longevity in populations of three scarids (*Scarus frenatus, S. niger,* and *Chlorurus sordidus*) and an acanthurid (*Acanthurus lineatus*) have been shown between mid- and outer-shelf locations on the northern GBR (Gust et al., 2001, 2002). Dudgeon et al. (2000) found evidence that high levels of genetic exchange occurred between populations of these fishes on mid- and outer-shelf reefs and concluded that observed differ-

Table 1

Distance strata and reefs sampled during September and October 2001 over the continental shelf of the central Great Barrier Reef near Townsville, Australia, for analyses of growth patterns, mortality, and size of the tropical damselfish *Acanthochromis polyacanthus*.

Distance strata	Reef sampled	Date(s) sampled	Average distance (km) to coast of the three sites ±SE
Inner shelf	Orpheus Island	4 and 5 Sep 2001	15.3 ±0.6
	Pandora Reef	3 Sept 2001	16.4 ±0.3
	Havannah Island	3 and 4 Sep 2001	25.1 ±0.3
Mid-shelf	Bramble Reef	15 Oct 2001	41.1 ±0.5
	Britomart Reef	16 Oct 2001	38.7 ±3.0
	The Slashers	20 Oct 2001	85.3 ±2.4
Outer shelf	Pith Reef	18 Oct 2001	74.4 ±0.9
	Barnett Patches	17 Oct 2001	62.6 ±1.8
	Myrmidon Reef	19 Oct 2001	110.4 ±0.8

ences in the demographic and life history features represented phenotypic plasticity.

Acanthochromis polyacanthus (Bleeker) is one of a few species of fish that are found in abundance at all distances across the Great Barrier Reef (Williams, 1982, 1983) and, therefore, was ideal for comparisons of cross-shelf patterns of demographic characteristics. *Acanthochromis polyacanthus* is a polymorphic gonochoristic pomacentrid and site-attached planktivore that inhabits reefs of the Indo-Australian Archipelago and adjacent regions (Allen, 1975). It is extremely wide spread and abundant along (north–south) the GBR (Williams, 1982, 1983). It is unusual among marine reef fishes and unique among damselfishes in that it lacks a dispersive planktonic larval stage (Robertson, 1973). Instead, adult *A. polyacanthus* lay demersal eggs and after hatching, both parents defend a brood of larvae and juveniles for several months (Robertson, 1973; Allen, 1975; Thresher, 1985a, 1995b; Kavanagh, 2000). In contrast to other taxa, therefore, dispersal is likely to be slow within and among reefs. *Acanthochromis polyacanthus* is one of the best studied coral reef fishes on the GBR with respect to predation (Connell, 1996, 1998, 2000), genetics and evolution (Doherty et al., 1994, 1995; Planes and Doherty, 1997a, 1997b), behavior (Robertson, 1973; Allen, 1975; Thresher, 1985a, 1995b; Nakazono, 1993; Kavanagh, 1998), reproductive success (Thresher, 1983), and early life history (Kavanagh, 2000), but no data exist on age, growth, and demographic parameters, such as mortality rates (but see estimates of juvenile mortality while larvae and juveniles are brooded by adults; Connell, 1996).

The objective of this study was to compare the demographic characteristics of *A. polyacanthus* across the continental shelf. Our approach was to sample replicate reefs in the central region of the GBR at multiple distance strata from shore (inner-, mid- and outer-shelf distances). In addition, we chose a section of the GBR where *A. polyacanthus* exhibited the same color pattern (brown anterior and white posterior) and are known to be genetically isolated (Planes and Doherty, 1997b). Any variation in demographic parameters, therefore, could be largely attributed to phenotypic plasticity. The specific objectives of this study were the following: 1) to validate the deposition of annual growth increments for fish of a wide range of sizes and ages by using tetracycline, 2) to describe patterns of growth of populations of *A. polyacanthus* within and among distance strata; 3) to describe the age and size structures of populations of *A. polyacanthus* within and among distance strata, and; 4) to calculate the instantaneous mortality and survival rates (Z) of populations of *A. polyacanthus* within and among distance strata.

Materials and methods

Study sites and sampling design

Spatial variation in demographics and structures of cross-shelf populations of *A. polyacanthus* was determined by using a partially hierarchical sampling design. Individuals of a wide range of sizes were collected from three replicate reefs within each of three distance strata (inner-, mid- and outer-shelf) spanning the width of the continental shelf of the central Great Barrier Reef near Townsville, Australia (Fig. 1, Table 1). At least 16 fish were collected with hand spears from each of three sites on each reef during September and October 2001. All fish collected were the same brown and white morph (Allen, 1975).

Sample processing

All fish were measured (standard length [SL] to the nearest mm) and weighed (to the nearest 0.01 g). Sagittal otoliths were extracted, cleaned in freshwater to remove the sagittal membrane, and allowed to dry

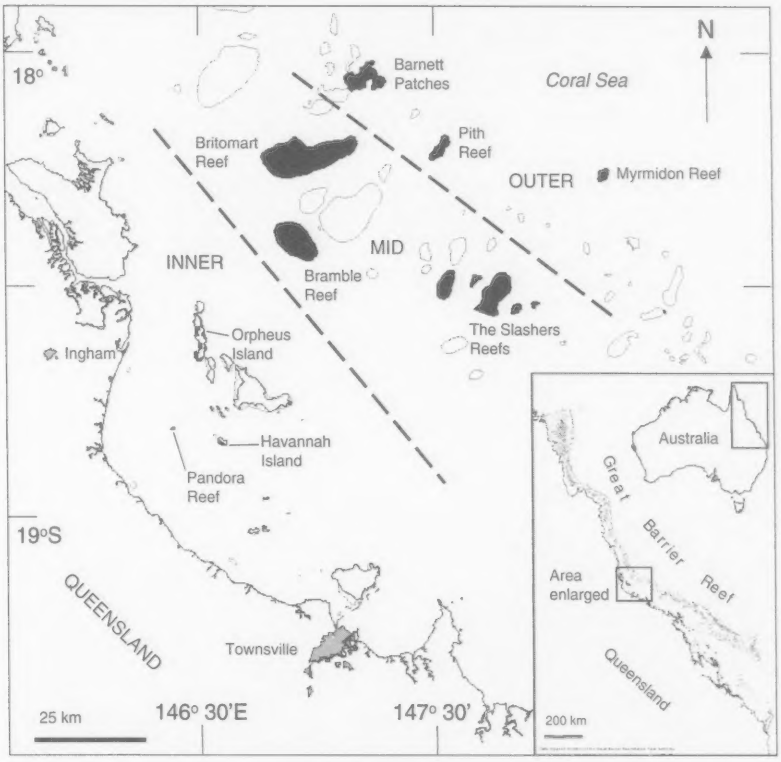

Figure 1

Map of the nine reefs on the central Great Barrier Reef where *Acanthochromis polyacanthus* were collected. Distance strata from the mainland (i.e. inner-, mid- and outer-shelf distances) are also indicated.

overnight. One otolith from each fish was then imbedded in Struers Epofix resin that was allowed to harden overnight in a drying oven at 60°C. A thin (250–300 μm) transverse section perpendicular to the long axis of the otolith was then taken through the core (primordium) of the otolith with a Buehler low-speed saw with two spaced diamond blades. This section was polished by hand with 9-μm lapping film to remove saw blade marks, thereby making the internal structure of the otolith more clearly visible. The polished section was then fixed to a labelled glass microscope slide with Crystal bond thermoplastic glue.

Analysis of growth increments

The opaque zones visible in the internal structure of the otolith were counted along a radius from the primordium to the outer edge of the largest sagittal lobe of the otolith with a compound microscope (Leica DMLB) and white incident light source. Alternating translucent and opaque increments were interpreted as annuli. Sections were coded and examined in random order and the opaque increments counted on two occasions by the same observer (JMH) separated by four weeks. Counts of annuli were compared between these two occasions in order to assess the confidence that could be placed in the interpretation of otolith structure. If increment counts differed by more than two between counting occasions, then the otoliths were re-examined. If, following a third reading, agreement between the third and one of the two other counts was not reached (all matching counts were used in analyses), then the otolith was not included in the analysis; 4.6% of otoliths were rejected on this basis (n=715 fish).

Validation of growth increments

The periodicity of growth increment formation was validated by marking a group of fish (of various sizes) reared in captivity with the antibiotic tetracycline hydrochloride (Sigma-Aldrich, Ballerup, Denmark). Small (known to be 0+ fish) and large fish were chosen to determine if annuli are formed early and late in life. Fish were held at the MARFU Aquarium Facility, James Cook University. For the duration of the experiment, the fish were held in several 70–500 L aquaria at this facility.

Adult fish were injected in the coelomic cavity with 0.05 g/mL tetracycline in sterile saline solution at concentrations equivalent to 0.05 g/kg body weight (McFarlane and Beamish, 1987). The approximate weight of each individual was estimated from the relationship between weight and SL. Juveniles were mass marked by immersion in a tetracycline solution (concentration: 0.5g/L) in seawater for 12 hours (overnight). The tetracycline generally forms a very effective time-marker in otoliths; it fluoresces when viewed under ultraviolet light (Geffen, 1992).

The experiment commenced in May 2002 and fish were sacrificed after six months, one year (June 2003), and one-and-a-half years (November 2003). Ten fish had readable otoliths for which validation was attempted. Otolith sections were viewed with a compound microscope and incident ultraviolet light in a darkened room. When a fluorescing tetracycline band was identified, its position in relation to the edge was measured. The section was then examined under reflected white light and measurements of increment widths and marginal increments were recorded. Known time at liberty, expressed as a proportion of one year, was then compared with estimated time at liberty by using the growth of the otoliths. If estimated time at liberty equalled actual time at liberty, it supported the hypothesis that opaque increments were deposited annually. Juveniles and adults were collected on each occasion to determine whether increments were deposited annually, early and late in life.

The length of time for increment formation was also estimated by calculating the number of days after tetracylcline treatment. The number of days after treatment was estimated by comparing the position of the tetracycline mark with that of the last (marginal) opaque increment and the width of a full annual increment with the following formula:

$$Number\ of\ days\ after\ treatment = \frac{TE - MI}{IW} \times 365,$$

where TE = otolith growth after treatment;
MI = the marginal increment; and
IW = the final full increment width.[1]

Growth

It was hypothesized that patterns of growth would vary with distance from the coast. Growth rates were described by using von Bertalanffy growth functions that provided the best fit to size-at-age data when compared with estimates of the Schnute growth function (Schnute, 1981). The von Bertalanffy expression for length at age t (L_t), as a function of time is

$$L_t = L_\infty\left[1 - e^{-K(t-t_0)}\right],$$

where L_∞ = the asymptote of the growth curve (average maximum length);
L_t = length at age t;
K = the rate at which the growth curve approaches the asymptote (L_∞);
t = age of fish in years;
t_0 = the theoretical origin of the growth curve (i.e., the hypothetical age of the fish when it has no length); and
e = the base of the natural logarithm.

Differences in growth curves for *A. polyacanthus* from each reef sampled were visualized by using the technique of Kimura (1980), where 95% confidence ellipses were generated around the parameter estimates of K and L_∞. Confidence ellipses that did not overlap indicated differences in growth parameters and enabled the pooling of data from sites within reefs at each distance stratum. The parameter t_0 was constrained to minus 0.05 to take into account the approximate size of *A. polyacanthus* at hatching (5 mm: Kavanagh, 1998, 2000).

Mortality

The instantaneous rate of mortality (Z) was calculated by using log-linear regression analyses of age-frequency data sets for *A. polyacanthus* populations from each reef (Pauly, 1984). With this method, recruitment was assumed to be consistent over time at each reef. The natural logarithm of the number of fish sampled from each age class was compared with their corresponding age. Year classes to the left of the age-frequency mode were excluded from the analysis because our sampling technique was biased against small *A. polyacanthus*. Fish greater than 60 mm were collected. The slope of the regression line between year classes estimated the instantaneous mortality rate (Z):

$$Z = F + M,$$

where F = fishing mortality; and
M = natural mortality (Gust et al., 2002).

Because there is no fishery for *A. polyacanthus* on the GBR, F equals zero and therefore Z estimates natural mortality only. Annual survival rate estimates were then calculated according to the equation $S = e^{-Z}$ (Ricker, 1975). Comparisons of the slopes of age-frequency relationships (for estimates of Z) were made by using analysis of covariance (ANCOVA) according to the procedures of Zar (1999). Data from each site were pooled for each reef because in many cases sample sizes were too small to provide reliable estimates of mortality at the site level. Similarities in mortality rates among replicate reefs within distance strata allowed us to pool data at the strata level so that comparisons of mortality between shelf positions could be made.

[1] We assumed similar IWs for fish older than 3 years. For fish 3 years or younger the IW was calculated as an average from all experimental fish.

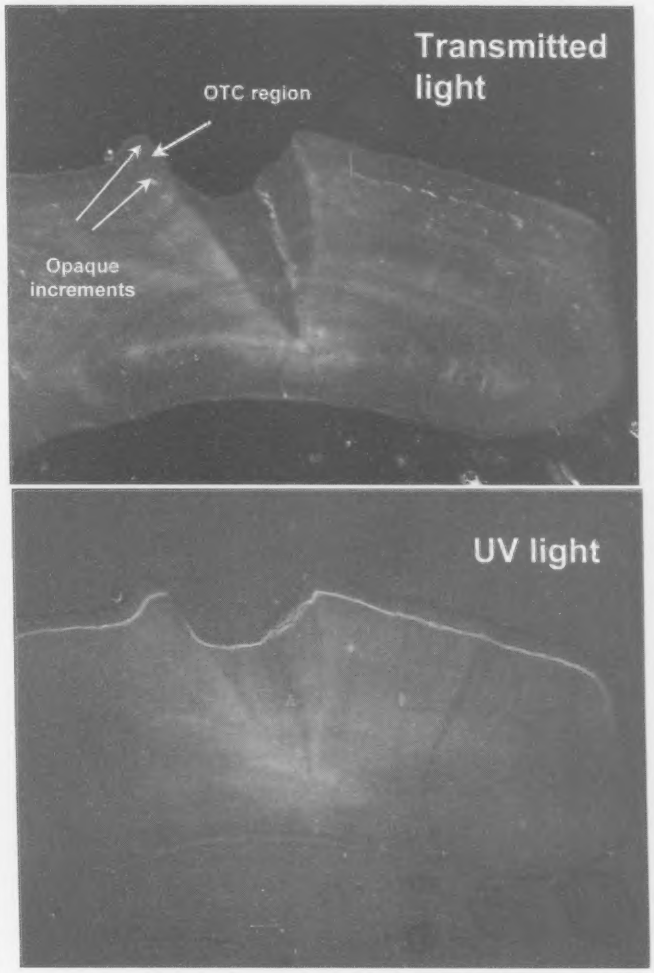

Figure 2

Photographs of sectioned *Acanthochromis polyacanthus* (age=5 years) otolith showing: (upper) alternating opaque (annuli) and translucent band pattern and (lower) the fluorescent tetracycline mark. Note the single opaque band following the tetracycline mark (time at liberty=380 days). OTC = oxytetracline.

Results

Age validation

All fish treated with tetracycline had clear fluorescent marks in their otoliths (Fig. 2). The positions of the fluorescent tetracycline bands in relation to the otolith margin were consistent with the deposition of opaque zones on an annual basis (Table 2). In general, percent agreement was over 75% (7/10 fish). Differences between actual and estimated time at liberty were probably related to slight variation in the small measurements that were made (i.e., fractions of a mm). The timing of deposition of the opaque increment was estimated to occur in spring because new increments were found at the edge of otoliths of fish that had been marked in May and sacrificed about 200 days later.

Size and age structures

There were large differences in the size-frequency distributions of fish sampled across the shelf (Fig. 3). At

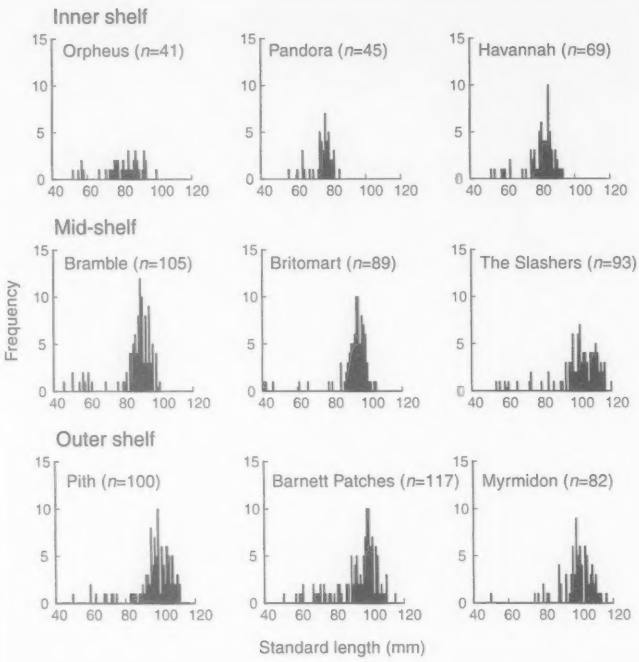

Figure 3

Size-frequency distributions for *Acanthochromis polyacanthus* collected from three reefs at each distance stratum from shore. Data were pooled for the three sites sampled at each reef.

inner-shelf reefs (n=155), only one fish >100 mm was collected. In contrast, between 38% and 54% of fish collected from outer-shelf reefs were >100 mm. A mix of inner- and outer-shelf size-frequency distributions was evident for mid-shelf reefs. Bramble and Britomart reefs had 1% and 7% of fish >100 mm, respectively, whereas The Slashers had the highest proportion of fish >100 mm collected of any reef (67%) including the largest individual fish collected (120 mm); however, this result was more characteristic of outer-shelf reefs. Another conspicuous feature of the cross-shelf size frequencies was the very narrow size range of adult fish collected on inner-shelf reefs in comparison to the size range of fish collected from mid- and outer-shelf locations (Fig. 3). Size selectivity due to the collection technique (hand spear) restricted the numbers of fish <60 mm that could be collected.

Maximum age of *A. polyacanthus* was similar at all reefs sampled (Fig. 4; inner shelf: 9–10 yr, mid-shelf: 9–10 yr, outer shelf: 10–11 yr). The largest age class of fish on the inner-and mid-shelf reefs comprised 3–4 year olds, whereas on the outer-shelf reefs, 2-year-old fish made up the largest proportion of the populations. The two oldest fish were both collected from outer-shelf reefs (Myrmidon and Barnett Patches) and were both 11 years old. Strong age-structured cohorts of fish were found at some reefs within the same distance stratum and these cohorts were found only at these reefs and distance stratum. For example, there were strong year classes at Pith and Barnett Patches in years 5 and 6 that were not found at Myrmidon (Fig. 4).

Growth

Variation in patterns of growth was greater among distance strata across the shelf than among reefs within a distance strata (Fig. 5). There was variation in growth between individuals from reefs within each shelf position and this resulted in variable size-at-age relationships (Fig. 5). From inner-shelf reefs, fish from Pandora showed small asymptotic sizes and thus had lower average L_∞, (L_∞=77.4 mm) compared to fish from Orpheus and Havannah (L_∞=87.0, 84.2 mm, respectively; Table 3). Distinct, non-overlapping ellipses formed in 95% confidence interval plots of L_∞ in relation to K confirmed that growth curves for fish from Pandora differed from those at Orpheus and Havannah (Fig. 5). Fish collected from mid-shelf reefs (Bramble, Britomart, and The Slashers) showed differences in growth among all reefs (non-overlapping 95% confidence ellipses; Fig. 5). Growth of fish

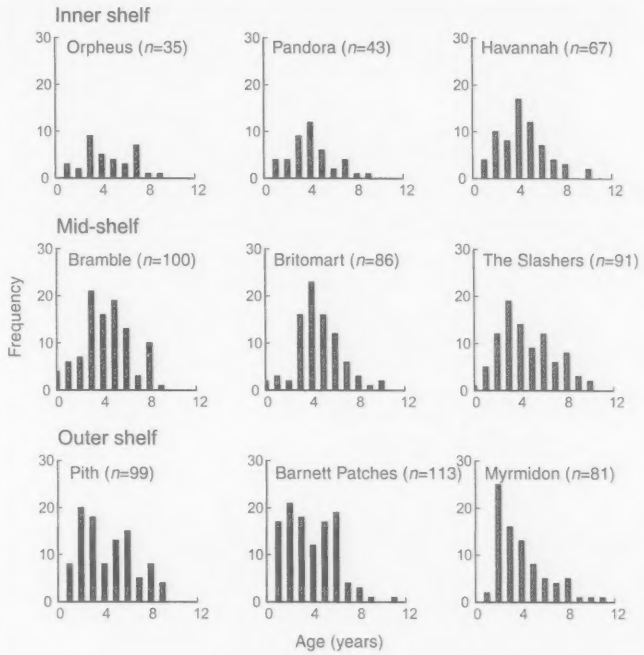

Figure 4

Age-frequency distributions for *Acanthochromis polyacanthus* collected from three reefs at each distance stratum from shore. Data are pooled from the three sites sampled at each reef. All age estimates were derived from counts of otolith annuli.

Table 2

Validation data with the use of tetracycline to determine the periodicity and timing of opaque ring deposition for *Acanthochromis polyacanthus* with the use of tetracycline as a time marker. TAL = time at liberty expressed as a proportion of one year and derived from growth measurements from reared fish treated with tetracycline. TC = tetracycline.

Fish age (yr)	TC to marginal increment (mm)	TAL (mm)	TAL as proportion of year	Estimated days from TC marking	Actual days from TC marking	Percent agreement = (estimated/actual × 100)
1	0.0423	0.30	0.43	110	158	69
1	0.0463	0.33	0.43	120	158	76
1	0.1784	0.94	0.97	344	355	97
5	0.0686	0.80	1.04	291	380	76
5	0.0739	0.83	1.04	304	380	80
5	0.1077	1.00	1.52	365	556	66
5	0.0805	0.81	1.52	295	556	53
6	0.1471	1.46	1.47	532	537	99
7	0.1034	0.90	1.12	327	409	80
7	0.0919	1.30	1.52	474	556	85

from the outer reefs (Pith, Barnett Patches, and Myrmidon), however, was similar for fish from each of these reefs (overlapping 95% confidence ellipses; Fig. 5).

Average maximum length (L_∞) varied across the shelf and differences among strata were generally greater than within-distance strata. The K values for all three

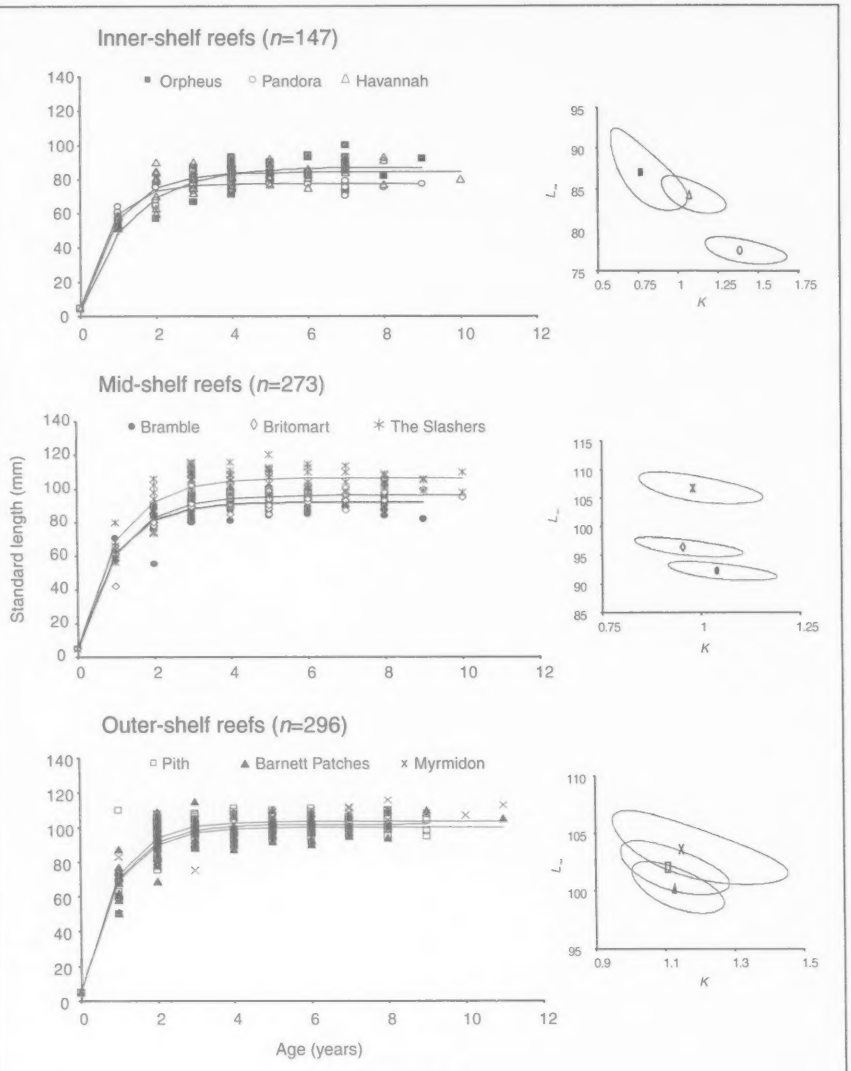

Figure 5

Von Bertalanffy growth curves for *Acanthochromis polyacanthus* collected from three reefs within each distance stratum. 95% confidence ellipses are given for the parameters K (growth coefficient) and L_∞ (mean asymptotic length).

shelf positions were similar and indicated that K values for *A. polyacanthus* converge at asymptotic sizes at approximately the same rate of growth, irrespective of proximity to the coast (Fig. 5 and Table 3). However, an obvious trend for increased L_∞ occurred with increasing distance from the coast (inner shelf: ~83 mm, mid-shelf: ~99 mm, outer shelf: ~102 mm). The growth parameters of fish from The Slashers were more similar to those of fish taken from the outer-shelf reefs than to those we defined *a priori* as mid-shelf (Fig.6). The Slashers are in fact much farther from the coast (85 km), as are Pith Reef (74 km) and Barnett Patches (63 km) on the outer shelf, than the other two mid-shelf reefs (Britomart: 39 km, Bramble: 41 km) (Fig. 1, Table 1).

Mortality

Mortality rates for *A. polyacanthus* did not differ significantly between replicate reefs within inner-shelf (test for slopes $df_{(2,19)}$, F=0.982, P=0.39), mid-shelf (test for slopes $df_{(2,19)}$, F=1.334, P=0.29) or outer-shelf (test for slopes $df_{(2,19)}$, F=0.658, P=0.53) locations (Table 4).

Age frequencies, therefore, were pooled at the shelf level (within distance strata; Fig 7).

Acanthochromis polyacanthus mortality rates did not differ significantly between the inner-, mid- and outer-shelf strata (test for slopes $df_{(8, 63)}$, F=0.367, P=0.70) (Fig. 6). Although mortality estimates were progressively lower with increased distance from the coast, this trend was not significant (inner shelf: −0.51, mid-shelf: −0.48, outer shelf: −0.43; Fig. 6, Table 4). Associated survival rate estimates (S) varied between reefs by ~9% per annum at inner- and mid-shelf strata and by ~6% per annum on the outer shelf (Table 3). The mean difference in survival rates for *A. polyacanthus* between the inner and mid-shelf was ~2% and between the mid- and outer shelf was ~3% (Table 4).

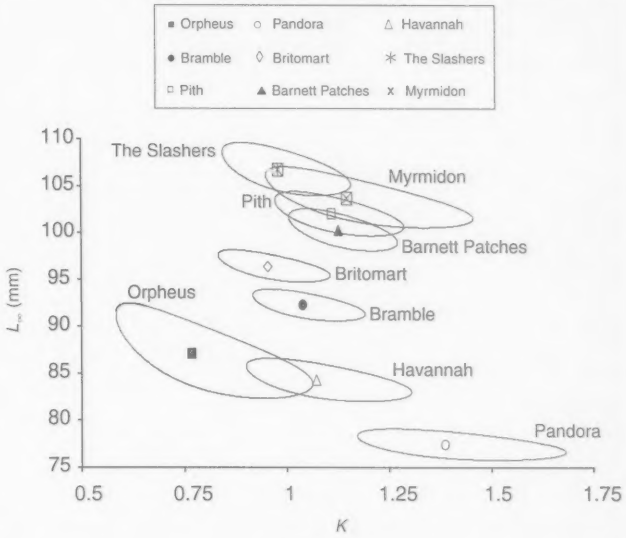

Figure 6

95% confidence ellipses for the von Bertalanffy growth parameters K (growth coefficient) and L_∞ (mean asymptotic length) for *Acanthochromis polyacanthus* from all reefs sampled.

Discussion

The demographic parameters of L_∞ and patterns of growth for populations of *A. polyacanthus* varied across the shelf on the central GBR. Although there was variation in body size and growth among reefs within a distance stratum, it was minor compared to overall cross-shelf patterns. In this study, mortality estimates and maximum age were similar for populations of fish across the shelf. Thus, in order to explain the cross-shelf trend in body size, fish must have grown faster with increasing distance from shore (Fig. 7, Table 1).

Despite the relative paucity of age-based studies on reef fishes (Choat and Robertson, 2002), variable rates of growth have been previously demonstrated for fish at local scales (hundreds of metres to kilometers: Fowler and Doherty, 1992), medium scales (kilometers to tens of kilometers: Choat and Axe, 1996; Hart and Russ, 1996; Newman et al., 1996; Meekan et al., 2001; Gust et al., 2002), and large scales (thousands of kilometers: Choat and Robertson, 2002). Gust et al. (2002) found that growth patterns of scarids varied between the reef crests of mid- and outer-shelf sampling locations on the northern GBR. In contrast to the results from the current study, however, outer-shelf populations of scarids had smaller asymptotic sizes and slower growth rates than mid-shelf populations. The factors influencing patterns of growth, therefore, vary by group.

Differences in the shape of growth curves between geographic regions or areas may be determined by both genetic and environmental influences (Sebens, 1987). Populations of reef fish are generally considered to be genetically open systems (Sale, 1991) and it is considered unlikely that adaptation of such populations to local conditions through genetic selection can occur (Warner, 1991). *Acanthochromis polyacanthus*, however, possesses a unique life history trait among reef fishes in that it lacks a dispersive larval phase. The major implication of this characteristic is the potential for genetic isolation of populations of these fish. Even reefs that are in relatively close proximity to one another (100's of m) may become "genetic islands" isolated by any barrier that proves impassable to adults (e.g., deep water). Without gene flow, reproductively isolated

Table 3

Parameters from von Bertalanffy growth models on the fishes collected from different distance strata and reefs.

Shelf location and reef	n	L_∞	K	r^2
Inner shelf				
Orpheus Island	36	87.03	0.77	0.83
Pandora Reef	44	77.43	1.39	0.92
Havannah Island	67	84.23	1.07	0.81
Mid-shelf				
Bramble Reef	97	92.24	1.04	0.83
Britomart Reef	85	96.37	0.95	0.87
The Slashers	91	106.73	0.98	0.75
Outer shelf				
Pith Reef	100	101.98	1.11	0.76
Barnett Patches	114	100.27	1.13	0.78
Myrmidon Reef	82	103.66	1.15	0.70

Table 4

Estimates of mortality (M) for fishes collected from different distance strata and reefs. Pooled values are for all reefs within one distance stratum. n = number of fish in sample. S = animal survival rate.

Reef	n	M	Pooled M	S (%)	Pooled S (%)
Inner shelf			0.51		60.0
Orpheus Island	30	0.29		74.8	
Pandora Reef	34	0.40		67.0	
Havannah Island	45	0.42		65.7	
Mid-shelf			0.48		61.8
Bramble Reef	83	0.44		64.4	
Britomart Reef	63	0.48		61.9	
The Slashers	73	0.34		71.2	
Outer shelf			0.43		65.1
Pith Reef	91	0.32		72.6	
Barnett Patches	96	0.40		67.0	
Myrmidon Reef	79	0.38		68.4	

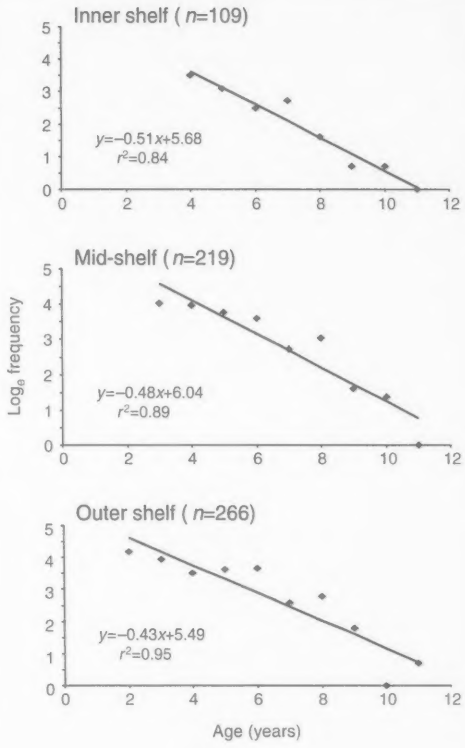

Figure 7

Age-based catch curve estimates of *Acanthochromis polyacanthus* mortality rates for reefs pooled by distance strata.

populations are expected to diverge over time with respect to their genetic composition (Doherty et al., 1994). Numerous studies have examined the genetic relationships between populations of *A. polyacanthus* on the GBR (Doherty et al., 1994, 1995; Planes and Doherty, 1997a, 1997b). Isozyme analyses of populations of different color morphs at various spatial scales have shown significant genetic variation at both the regional (1000's of km) and local (100's of m) level, which under normal circumstances would suggest separate species for each color morph (Doherty et al., 1994; Planes and Doherty, 1997a). However, differences in the growth rates of *A. polyacanthus* across the continental shelf in this study are unlikely to reflect genetic differences between the populations sampled because all individuals collected were of the same color morph and were from a relatively small area (about 400 km^2, *cf.* 450,000 km^2 for the entire GBR).

Environmental influences that can affect patterns of growth include predation pressure, temperature, and related effects on metabolism, variations in resources (e.g., abundance of planktonic food), and variation in water condition (e.g., turbidity).

High rates of predation may "drive" faster growth (Werner, 1984), or conversely, select for early maturation and smaller adult size (Reznick et al., 1990; Hutchings, 1997). It is unlikely that the cross-shelf patterns in growth that we found were determined by differences in mortality rates. Some data on serranid abundance (Williams, 1982) and anecdotal accounts have indicted that predator abundance is greatest on mid- and outer reefs of the GBR (Gust et al., 2001). Our measures of instantaneous mortality (Z) and age maximum, however, did not vary with distance from the mainland. Furthermore, in contrast to the patterns that Gust et al. (2001) found for scarids, L_∞ increased with distance from the coast. Mortality rates have been shown to vary among locations within reefs for several species of coral reef fish (Aldenhoven, 1986; Eckert, 1987; Sale and Ferrell, 1988; Beukers and Jones, 1997) including *A. polyacanthus* juveniles (Connell, 1996), as well as over larger spatial scales (Meekan et al., 2001; Gust et al., 2002). In contrast to these last two studies, particularly that of Gust et al. (2002), mortality rates for *A. polyacanthus* were similar at all three cross-shelf strata. We acknowledge, however, that no data were available on mortality rates of fish from zero to two years of age. It is possible that mortality rates do vary with distance from shore over this age range.

An increase in adult size may occur when individuals experience a decline in average temperature during development (Atkinson, 1994). It is also well established that metabolism and growth are increased at higher ambient temperatures in ectotherms (Schmidt-Nielsen, 1990). Differences in temperature between the water bodies spanning inner-, mid- and outer-shelf positions in the central GBR do occur; relatively shallow near-

shore waters are the warmest and outer-shelf waters are the coolest (Wolanski, 2001). The opposite pattern of growth to the one observed in this study would be predicted by this cross-shelf gradient in water temperature. It is also considered unlikely that local upwelling events on outer-shelf reefs could produce the observed differences, but they could influence primary productivity and abundance of food (zooplankton) through nutrient-rich waters. An increase in average annual temperature correlates with maximum age in some fishes (review Choat and Robertson, 2002), but we found no differences in age maximum across the shelf. We conclude that any differences in temperature across the shelf are not persistent enough to affect cross-shelf patterns of growth of *A. polyacanthus*.

Differences in growth profiles can be more realistically attributed to cross-shelf variation in some limiting resource(s). This variation in resources may influence the quality and quantity of food, suitable nest sites, refuges from predators and (or) wave exposure, and density of conspecifics and (or) other species that compete with *A. polyacanthus* for resources. Correlative studies have concluded that the distribution and abundance of coral reef fishes is strongly influenced (directly and indirectly) by physical factors such as wave exposure, sediment loads, water depth, and topographical complexity, as well as by biological factors (Williams, 1982). These factors also have the potential to affect growth rates.

A combination of reduced resource levels and high population densities on outer-shelf reefs strongly indicated that growth profiles represent density dependence in scarids (Gust et al., 2001, 2002). Density of con- and hetero-specifics was not recorded for our study, but densities of *A. polyacanthus* were clearly greatest on the mid- and outer-shelf reefs. This observation is contrary to the pattern noted by Williams (1982) who found greatest abundances of *A. polyacanthus* on inner- and mid-shelf reefs. Thresher (1983) suggested that food abundance is a limiting resource for *A. polyacanthus* and interspecific competition for food does occur. Thus, it is plausible that variation in abundance of and competition for food across the shelf may have influenced the growth rates observed in the present study. The large differences in cross-shelf densities and L_∞'s of *A. polyacanthus* indicate that competition may be less important than variation in quantity and quality of food across the shelf.

Biomass of planktivores is generally highest at mid-shelf reefs on the central GBR (Williams and Hatcher, 1983). Although data on cross-shelf abundance and distribution of plankton are limited, Williams and Hatcher attributed this pattern to the increased availability of food (zooplankton) in mid-shelf waters. Upwelling of cold, nutrient-rich water from the edge of the continental shelf results in high biomasses of phytoplankton. Aging of the water (time since upwelling) is accompanied by a shift in dominant planktonic biomass to herbivorous and then carnivorous zooplankton. This shift in biomass composition occurs simultaneously with the prevailing wind-driven passage of water across the shelf and ultimately leads to the greatest biomass of zooplankton occurring in mid-shelf waters (Andrews and Gentien, 1982; Sammarco and Crenshaw, 1984; Williams et al., 1988). Food quality has also been previously shown to limit growth and reproduction in herbivorous coral reef fishes (Horn, 1989; Choat, 1991).

Despite a high abundance of zooplankton near shore, these waters also have higher turbidity than mid- and outer-shelf reefs. Visual impairment caused by very turbid waters may hinder the ability of fish to feed on planktonic organisms and this hypothesis has been suggested as a factor contributing to the low relative abundances of planktivorous fish on inner-shelf reefs (Williams et al., 1986). It is possible that this factor may retard the growth and influence the maximum size of planktivores like *A. polyacanthus* by effectively reducing food availability. Interestingly, lowest L_∞ values were found at the most turbid inshore reef, Pandora. Lower visibility near shore, however, did not appear to affect the mortality rates of *A. polyacanthus* at inner-shelf reefs.

There were clear differences in growth, size maxima, and age structures for populations of *A. polyacanthus* across the continental shelf of the central GBR. Although *Acanthochromis polyacanthus* grew faster and to a larger size with increasing distance from the mainland, cross-shelf mortality rates and maximum ages were similar. Because these populations of fish are unlikely to be genetically distinct, we suggest that biotic and physical processes are the most plausible cause of these cross-shelf patterns. Increased abundance of zooplankton in mid- and outer-shelf waters, coupled with potential visual impairment associated with high turbidity levels on the inner shelf, are likely mechanisms that explain the observed patterns, but multifactorial manipulative experiments are required to determine the relative contribution of these factors to variation in demographic parameters. Our study therefore cautions against pooling demographic parameters over broad spatial scales without considering cross-shelf variation.

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Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration

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Abstract—Aspects of the feeding migration of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea (EBS) were investigated by examining the relationship between temperatures and densities of fish encountered during acoustic and bottom trawl surveys conducted in spring and summer between 1982 and 2001. Bottom temperature was used as an indicator of spring and summer warming of the EBS. Clusters of survey stations were identified where the density of walleye pollock generally increased or decreased with increasing water temperature. Inferences about the direction and magnitude of the spring and summer feeding migration were made for five length categories of walleye pollock. Generally, feeding migrations appeared to be northward and shoreward, and the magnitude of this migration appeared to increase with walleye pollock size up to 50 cm. Pollock larger then 50 cm showed limited migratory behavior. Pollock may benefit from northward feeding migrations because of the changes in temperature, zooplankton production, and light conditions. Ongoing climate changes may affect pollock distribution and create new challenges for pollock management in the EBS.

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Fish. Bull 103:574–587 (2005).

Walleye pollock (*Theragra chalcogramma*; referred to as "pollock" in this article) migrate seasonally. Such migrations have been described for the northern Sea of Japan (Maeda, 1986; Maeda et al., 1988, 1989; Kooka et al., 1998), Korean waters (Shuntov et al., 1993), the Okhotsk Sea (Shuntov et al., 1987), and the western and central Bering Sea (Fadeyev, 1989; Bulatov and Sobolevskiy, 1990; Efimkin, 1991; Radchenko and Sobolevskiy, 1993; Shuntov et al., 1993; Balykin, 1996). Generally, these authors have described a spring and summer migration from spawning grounds to forage areas (referred to as a "feeding migrations" by many authors) and a winter migration of pollock returning to spawning grounds (e.g., Maeda et al., 1988; Radchenko and Sobolevskiy, 1993). This pattern of migration is believed to occur in the eastern Bering Sea (EBS) where it has received considerable attention (Takahashi and Yamaguchi, 1972; Francis and Bailey, 1983; Pola, 1985; Shuntov, 1992; Shuntov et al., 1993; Stepanenko, 2001), but the evidence for this pattern of migration is sparse. In addition, there is a lack of information on the magnitude of, routes of, and size-dependent differences in seasonal migrations.

Temperature (and other factors closely related to temperature) affects the distribution and movements of pollock. Pola (1985) simulated temperature-induced migrations of pollock in the EBS occurring during May and June. Pollock appear to avoid some temperatures (Swartzman et al., 1994) and prefer environmental conditions that are linked to food availability associated with temperature gradients and fronts along the EBS slope (Swartzman et al., 1995). Water temperature is an especially important indicator of the transition from winter conditions to those supporting a spring bloom of phytoplankton and then zooplankton. In the EBS, the simulated onset of the feeding migration of pollock was delayed in colder years (Pola, 1985).

Annual surveys documenting the spatial distribution of fishes in relation to water temperatures can be used to infer details about their migratory behavior. Using annual survey data, Mountain and Murawski (1992) found that the relationship between the distribution of seasonally migrating species and water temperature could indicate a change in the overwintering location of the fish, or a change in the timing of the spring migration, or both. In the eastern Bering Sea, bottom trawl (BT) surveys and echo-integration-trawl (EIT) surveys are conducted in late spring and summer (Honkalehto et al[1]; Acuna et al.[2]), when water tem-

[1, 2] *See next page for footnote texts.*

peratures are generally rising on the eastern Bering Sea shelf (Overland et al., 1999; Stabeno et al., 2001). Interannual variability in climatic conditions and survey timing create variability in mean water temperatures encountered during the surveys (Acuna et al.[2]).

We describe the variability in distribution of pollock with temperature and propose that this variability may be explained by the fact that pollock migrate to feeding grounds during spring and summer. Temperature is used in our study as an indicator of how far into an idealized seasonal warming cycle each survey has occurred. Thus, the distribution of pollock observed in a warm year would be considered to be representative of that seen later in a seasonal warming cycle in a cold year. Generally, feeding migrations appeared to be northward and shoreward, and the magnitude of this migration appeared to increase with walleye pollock size up to 50 cm. Pollock larger then 50 cm showed limited migratory behavior. Pollock may benefit from northward feeding migrations because of the changes in temperature, zooplankton production, and light conditions.

Figure 1

Locations of AFSC bottom trawl stations (dots) and echo-integration survey transects (lines) in the eastern Bering Sea where walleye pollock (*Theragra chalcogramma*) were collected during bottom trawl surveys and echo-integration trawl surveys in spring and summer between 1982 and 2001.

Materials and methods

Data used in this investigation were collected by BT and EIT surveys conducted by the Alaska Fisheries Science Center.

Since 1982, BT surveys have been conducted annually over a standard area of the EBS, at the centers of 20×20 nautical-mile grids (Fig. 1). The corners of the grid block were also sampled in areas surrounding St. Matthew Island and the Pribilof Islands. The same standard trawl (83-112 eastern otter trawl) was used every year (Acuna et al.[2]) and surveys usually began in late May or early June, and ended in August. Surveys always began in the northeastern corner of the Bristol Bay and proceeded westward. Samples were collected by towing for 30 minutes at 1.54 m/s (intended speed). Temperature data were collected during each tow using an expendable bathythermograph (XBT) until 1992 and after 1992 with a micro-bathythermograph (MBT) attached to the headrope of the trawl. Catches were sorted by species and weight; number of fish caught and length-frequency data were collected for each tow.

Echo integration trawl survey transects were designed to coincide with north-south lines of BT stations. Similar to the BT survey, the EIT survey began also in the eastern Bristol Bay and proceeded westward. The time lag between the survey varied from 0 to 30 days. Acoustic data were collected with a Simrad EK500 quantitative echo sounding system. Biological

[1] Honkalehto, T., N. Williamson, and S. de Blois. 2002a. Echo integration-trawl survey results for walleye pollock (*Theragra chalcogramma*) on the Bering Sea shelf and slope during summer 1999. U.S Dep. Commerce, NOAA Tech. Memo. NMFS-AFSC-125,77 p.

[2] Acuna, E., P. Goddard, and S. Kotwicki (compilers). 2003. 2002 bottom trawl survey of the eastern Bering Sea continental shelf. AFSC Processed Report 2003-01, 169 p. Alaska Fish. Sci. Cent., NOAA Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA 98115.

data were collected by midwater trawl, bottom trawl, and Methot trawl (see Honkalehto et al.[1] for details). Pollock length data from trawls were aggregated into analytical strata based on echosign type, geographic proximity of hauls, and similarity in size composition of hauls. Estimates of numbers of pollock by size were derived by scaling acoustic measurements with the target strength-to-length relationship described in Traynor (1996). Temperature data were collected with an MBT mounted on the headrope of the trawl, although many of the profiles did not reach bottom because the trawls usually targeted midwater fish aggregations. For that reason, we elected not to use the temperature data collected during the EIT survey. Because both surveys were conducted at approximately the same time of year, we used the mean bottom temperature from the BT survey as an index temperature for the EIT survey. We used EIT data collected in years 1994, 1996, 1997, 1999, and 2000.

Because of the semidemersal nature of pollock (Bailey et al., 1999a) and assuming that pollock do not dive as a boat and trawl approaches, BT data are assumed to describe the demersal part of the pollock stock within 3 m of the bottom. EIT data represented the midwater part of the stock from 3 m above the bottom to 14 m below the surface. In our calculations, we used two density measures: CPUE in kg/ha for the BT data and biomass (tons) per 20-mile square for EIT data (the term "density" will be used in the present study to refer to both of these measures). Echo integration trawl survey 20-mile squares were centered on the BT survey stations, so that both sets of data could be easily compared (the term "station" will be used here to refer to BT survey stations as well as EIT survey squares). Because of known age-dependent behavioral differences between pollock (e.g., Shuntov et al., 1993; Bailey et al., 1999a), we investigated five different length classes of pollock; up to 20 cm (mostly 1-year-old pollock), 21–29 cm (mostly 2-year-old pollock), 30–39 cm, 40–49 cm, and pollock >50 cm. Because of differences in the year-class strengths between years, we scaled the data by dividing the density data for each station by the average fish density for each year within each length class. Thus, a station with a density value of 1 has an average density for a given year and a station with a value of 5 has a density 5 times larger for a given year.

If the pollock distribution in the EBS is assumed to be dynamic and related to temperature, the relationship between temperature and pollock density will be different at each spatial location. This means that if pollock moved from location A to location B over a period of rising temperatures, we expected a negative relationship between density and temperature in location A and an offsetting positive relationship in location B. To study these relationships in the EBS, we applied a two-step approach. In the first step, we identified possible locations where pollock density may be changing with temperature. In the second step, we identified locations of most significant biomass changes with temperature and quantified these changes.

First step—identifying areas of change in fish density with temperature

For both types of surveys, we calculated the slope of the linear regression of scaled density against bottom temperature for each station over the time series (e.g., a slope value of 1 indicates an increase of 1 unit of density per degree increase of temperature). Slopes in the range between –0.3 and 0.3 were ignored because they represented areas of low fish density or areas of no significant changes in fish density between years. Each station slope was then plotted on a map to visualize the spatial relationship between these two variables for the BT and EIT surveys.

To contour areas with similar slopes, we interpolated the data using inverse distance-weighted squared interpolation (IDW). This method was chosen because IDW is an exact interpolator, where the maximum and minimum values in the interpolated surface can occur only at sample points and values at all sampling points are true measured values (ArcGIS, Geostatistical Analyst Help, 2003, ESRI, Redlands, CA). Using these maps, we identified the main spatially correlated clusters of stations with positive or negative slopes of the linear regression of pollock density against temperature (Figs. 2 and 3). Stations were assigned to clusters visually by using slope maps that overlapped the stations map. For practical reasons we investigated only clusters with four stations or more. Twenty-eight clusters were identified for BT survey and 17 clusters were identified for EIT survey (Figs. 2 and 3).

Second step—identifying areas of most significant changes in biomass with temperature and quantifying these changes

For each cluster, we calculated mean temperature and percentage of total biomass of pollock present in this cluster in each year. Total biomass and biomass within clusters were calculated as outlined in Wakabayashi et al. (1985). The relationship between mean bottom temperature and percentage of pollock biomass within each cluster was then fitted to a linear regression model. Because the error variances for the BT survey were not constant (variance increased with fish density), we weighted the regression by the inverse of the variance (Neter et al., 1996). For the EIT survey, we made no assumptions about the variance that was due to a small number of observations (only five years of data).

The relative strength of the relationship between the percentage of pollock biomass and temperature within each cluster was characterized by the P-value of the slope (Table 1) (the P-values are not a true measure of statistical significance because the stations were not chosen randomly). Only clusters with the strongest relationships were used in the interpretation of results. Because the number of data points (years) in each analysis was equal within the survey (BT surveys—20 points, EIT surveys—5 points), P-values indicate relative strength of the temperature-biomass relationship. We plotted histograms of P–values for

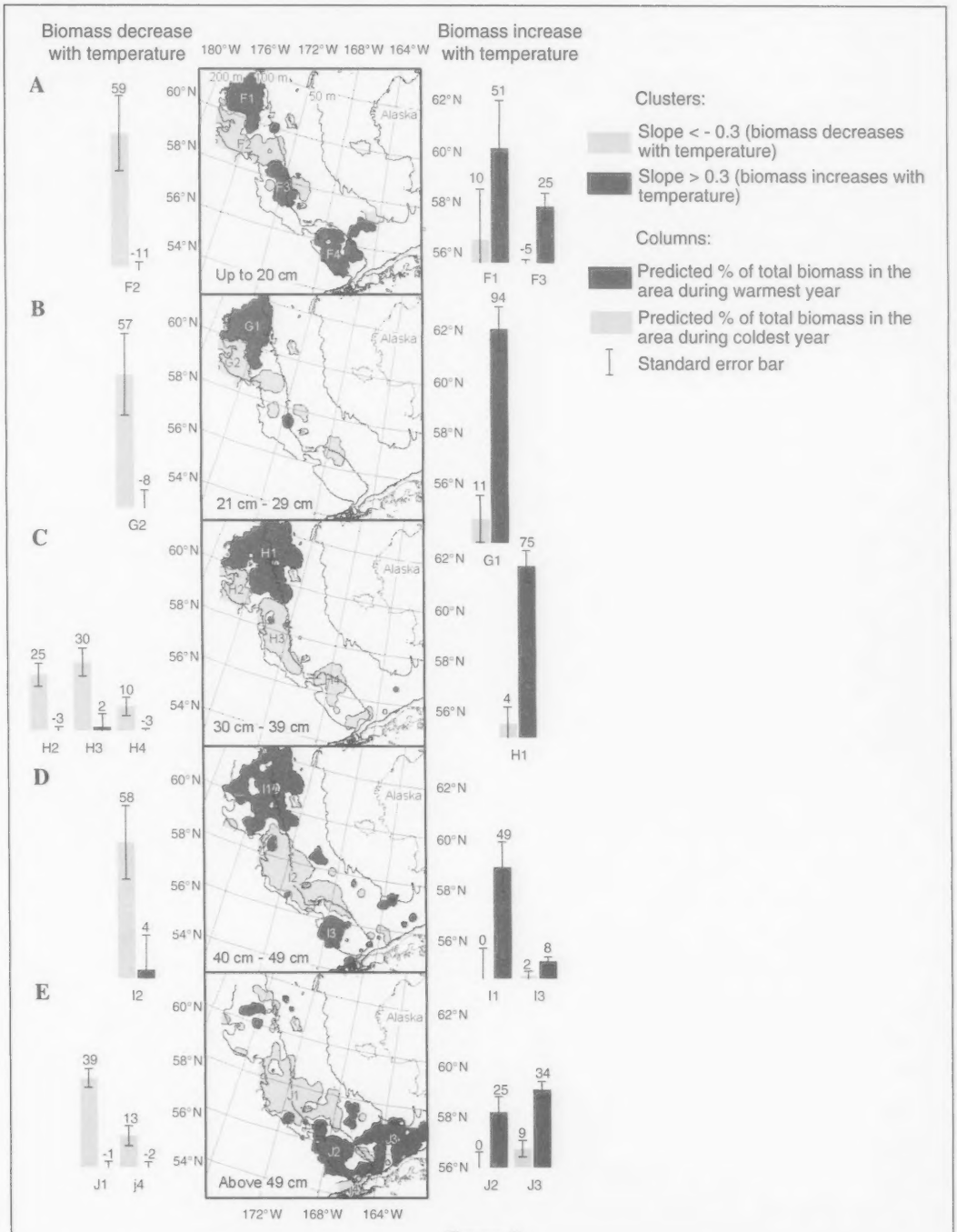

Figure 2

Clusters of positive and negative slopes of the linear regression of pollock (*Theragra chalcogramma*) density (detected by echo-integration trawl survey) when plotted against temperature. Columns represent predicted percent biomass of fish in these clusters within the observed range of temperatures. Predicted percent of biomass is shown only for clusters with the strongest relationship between temperature and fish density with the exception of cluster F1 (see results for explanation). Labels are located at the geographic centers of the clusters.

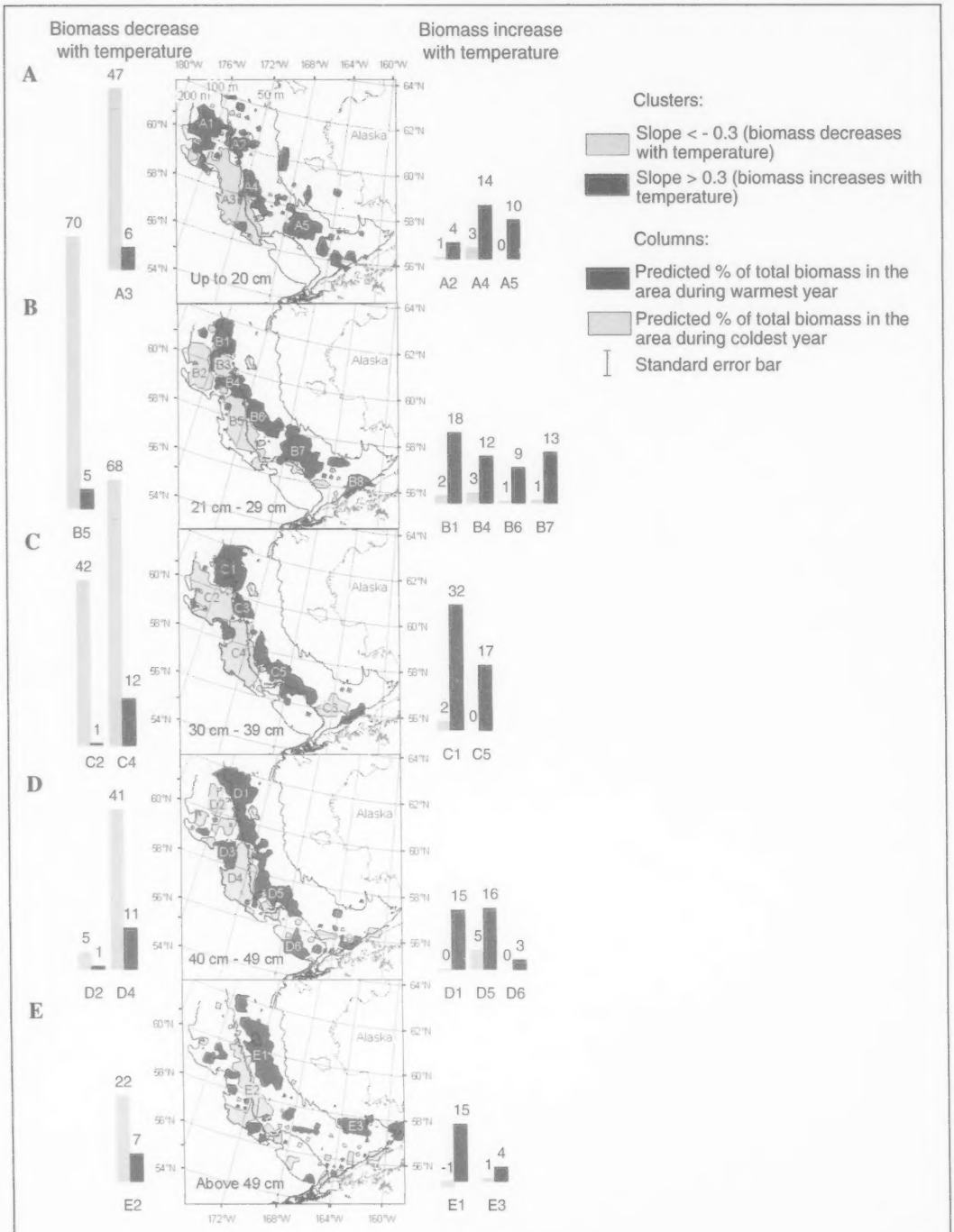

Figure 3

Clusters of positive and negative slopes of the linear regression of pollock (*T. chalcogramma*) density (detected by bottom trawl survey) when plotted against temperature. Columns represent predicted percent biomass of fish in these clusters within the observed range of temperatures. Predicted percent of biomass is shown only for clusters with the strongest relationship between temperature and fish density.

Table 1

Results of linear regression analyses and predicted percent of total biomass in each cluster within an observed range of temperatures.

Cluster	Slope	Standard error of slope	Intercept	r^2	P	Percentage at min. temperature	Standard error of min. percentage	Percentage at max. temperature	Standard error of max. percentage
Botton trawl survey									
A1	3.0706	4.579	7.2013	0.024	0.511	8.82	5.07	15.49	4.89
A2	1.1579	0.382	1.6145	0.338	0.007	0.55	0.36	4.31	1.01
A3	−24.0232	6.812	98.8454	0.409	0.002	47.04	5.33	5.79	6.38
A4	3.3081	1.254	2.9747	0.279	0.017	3.14	1.22	13.75	2.84
A5	2.7928	0.837	−0.5577	0.382	0.004	0.08	0.47	10.13	2.65
B1	6.2744	1.655	4.5969	0.444	0.001	1.98	1.21	18.30	3.13
B2	−5.7916	3.445	24.2379	0.136	0.110	21.73	6.37	5.44	3.34
B3	−0.2449	0.839	4.9690	0.005	0.774	4.86	2.07	4.07	0.70
B4	3.6720	1.880	1.4972	0.175	0.066	2.83	0.52	12.05	4.33
B5	−26.2623	7.642	106.0603	0.396	0.003	70.17	14.89	5.08	4.06
B6	1.9462	0.756	2.9913	0.269	0.019	0.62	1.12	9.27	2.31
B7	3.4809	1.408	−0.5292	0.253	0.024	0.77	0.23	13.03	4.94
B8	0.5026	0.350	0.0979	0.103	0.168	0.10	0.44	2.47	1.30
C1	10.9174	2.355	10.7957	0.544	0.000	2.28	0.31	32.32	6.32
C2	−17.9173	5.809	60.4987	0.346	0.006	42.49	7.89	0.51	5.72
C3	1.1807	0.731	1.5962	0.127	0.124	0.84	1.20	4.68	1.26
C4	−26.8246	7.771	116.1162	0.398	0.003	68.32	10.03	12.06	6.27
C5	5.3395	1.413	−3.3847	0.442	0.001	0.11	1.79	16.77	2.65
C6	−1.4934	0.843	6.3588	0.148	0.094	4.77	2.07	0.89	0.28
D1	5.4677	1.368	7.2510	0.470	0.001	−0.15	0.44	15.42	3.55
D2	−1.9038	0.850	5.7227	0.218	0.038	4.50	1.39	0.87	0.45
D3	0.9668	2.954	2.9573	0.006	0.747	4.89	1.28	6.65	4.19
D4	−14.3609	5.356	65.9267	0.285	0.015	41.08	8.45	10.70	2.89
D5	3.6882	1.411	2.7672	0.275	0.018	4.92	1.18	15.81	3.02
D6	2.3974	0.830	−8.0125	0.317	0.010	0.04	0.31	2.60	0.81
E1	4.5778	0.733	6.1399	0.684	0.000	−1.45	1.13	14.86	1.56
E2	−5.7776	1.910	26.8244	0.337	0.007	22.13	3.71	7.32	1.24
E3	0.6479	0.217	0.9447	0.332	0.008	0.91	0.28	3.80	1.01
Echo-integration trawl survey									
F1	16.0479	13.649	−1.2116	0.315	0.324	10.35	21.80	51.49	20.57
F2	−27.5255	9.304	79.2218	0.744	0.059	59.39	14.86	−11.18	14.02
F3	11.7970	3.622	−13.4672	0.779	0.047	−4.97	5.76	25.28	5.46
F4	5.1896	8.463	−3.8753	0.111	0.583	−0.13	13.52	13.17	12.75
G1	32.3770	4.047	−12.0017	0.955	0.004	11.32	6.46	94.33	6.10
G2	−25.5850	10.151	75.6302	0.679	0.086	57.20	16.22	−8.40	15.30
H1	28.0501	4.012	−16.7011	0.942	0.006	3.51	6.41	75.42	6.05
H2	−10.6961	2.999	32.2026	0.809	0.037	24.50	4.79	−2.93	4.52
H3	−11.0388	3.249	38.1076	0.793	0.042	30.16	5.19	1.85	4.90
H4	−5.0998	2.465	13.8907	0.587	0.130	10.22	3.94	−2.86	3.71
I1	19.1934	7.184	−13.8822	0.704	0.075	−0.06	11.48	49.15	10.83
I2	−21.2245	8.449	73.6602	0.677	0.086	58.37	13.50	3.95	12.73
I3	2.3497	1.169	−0.0335	0.573	0.138	1.66	1.87	7.68	1.93
J1	−15.6292	2.465	50.1504	0.930	0.007	38.89	3.94	−1.18	3.72
J2	9.6097	4.374	−6.9678	0.616	0.115	−0.04	6.99	24.59	6.59
J3	9.7424	1.675	1.5600	0.918	0.010	8.58	2.68	33.56	2.53
J4	−5.8055	2.571	17.1422	0.629	0.109	12.96	4.11	−1.92	3.88

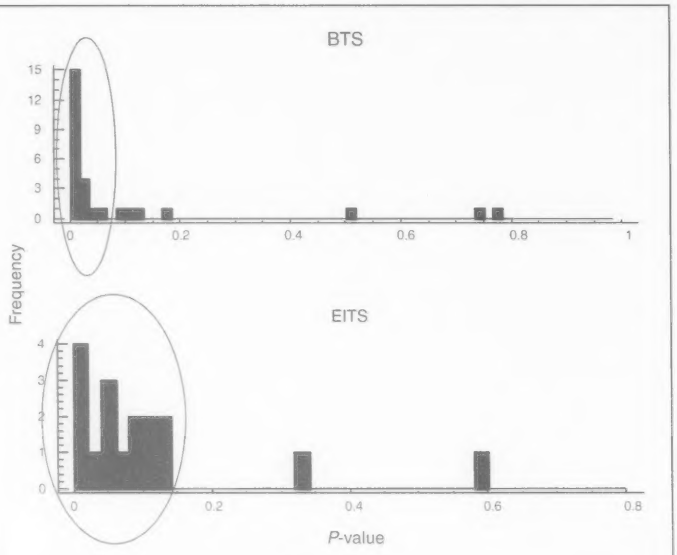

Figure 4

Histograms of *P*-values of linear regression between fish density and temperature calculated for all clusters. Circled bars represent the clusters with strongest relationship.

each survey (Fig. 4) and the groups of clusters with the strongest relationships between fish biomass and temperature were chosen for further investigations. These groups consisted of 21 clusters from BT surveys with *P*-values between 0.000 and 0.066 and 15 clusters from EIT surveys with *P*-values between 0.004 and 0.138. Using linear regression models (biomass against temperature), we calculated the predicted percentage of the total pollock biomass for each of these clusters (Table 1) within the temperature range observed during surveys (Fig. 5).

To evaluate a spatial scale on which biomass redistribution occurred for the EIT surveys, we calculated mean distance between clusters of negative and positive slope (Table 2). To obtain these values, we generated 100 random points within each of the clusters and calculated the mean distance between all possible pairs of points from both clusters. We did not attempt to calculate this distance for the BT surveys because of the much more complicated nature of the BT cluster maps.

Results

Northward and inshore shifts in pollock distribution in warmer years were found in the EBS for all length categories. The location and magnitude of these shifts and distance between clusters differed with the survey type and length categories. In the present study we address changes in pollock distribution by length category within each survey.

Table 2

Mean distance between largest echo-integration trawl (EIT) survey clusters. Clusters for pollock >50 cm were not calculated because of low selectivity of the EIT survey for these fish.

Clusters	Mean distance (km)	99% confidence interval (km)
F2–F1	241.3	2.3
G2–G1	217.5	2.5
H4, H3, H2–H1	368.3	4.7
I2–I1	453.7	3.9

Echo-integration trawl survey

The biomass of pollock <20 cm in cluster F2 near Zemchung Canyon at latitude 59°N decreased (with increasing temperature) from about 59% of the total biomass of pollock in the coldest year to 0% in the warmest year (Fig. 2A). This decrease was partially offset by the increase in pollock biomass in area F3, northwest of the Pribilof Islands. The relatively weak relationship (*P*-value=0.324) between pollock biomass and temperature in cluster F1 (north of F2) was caused by the extremely high abundance of <20 cm pollock within cluster F4 during 1997. Therefore the percentage of total

biomass was particularly low in clusters F1, F2, and F3 for that year. In cluster F1 we observed an increase in biomass from 10% to 51%.

For pollock 21–29 cm, changes between cluster G2 and G1 resembled changes between clusters F2 and F1. The percentage of total biomass in these two clusters changed from 57% to 0% and from 11% to 94%, respectively (Fig. 2B).

A slightly different situation was observed for pollock 30–39 cm (Fig. 2C). We identified three clusters of decreasing biomass with temperature: H2, H3, and H4 located, respectively, northwest of Zhemchug Canyon, northwest and east of the Pribilof Islands. Overall predicted biomass change in H2, H3, and H4 decreased from 65% to 2%. The offset for this negative change was found in cluster H1, where we noted a positive change from 4% to 75%.

Areas with decreasing fish biomass for pollock 40–49 cm were located within cluster I2 (Fig. 2D). Biomass decreased from 58% in the coldest year to 4% in the warmest year. We observed temperature-related increases in biomass mostly north of I2 in cluster I1 (0%–49%).

A quite different situation was observed for pollock >50 cm (Fig. 2E). Although pollock of this size seemed to concentrate northwest and northeast of the Pribilof Islands (similar to pollock 30–49 cm) during cold years; in warm years they were found in EIT surveys mainly in the southeast, as opposed to the smaller fish that are found mainly in the north. Results for pollock >50 cm should be treated cautiously because only a very small part of the entire population of pollock this size can be detected with the EIT survey (Ianelli et al.[3]). Because of the benthic habits of pollock >50 cm (Shuntov et al., 1993), most were detected in BT surveys.

Overall, our analysis of EIT survey data indicated a northward temperature-related shift of 50–80% of pollock <50 cm in two major areas. With increasing temperature, the density of pollock <40 cm decreased northwest of Zhemchug Canyon in a large area at 100 m to 200 m depths. Similarly, the density of pollock 30–49 cm decreased northwest of the Pribilof Islands. Offsetting these decreases, pollock density increased in the northernmost area of the survey (close to the U.S.-Russia Convention Line).

Although the direction of the shift was the same for all length categories up to 50 cm, the mean distance between the clusters with negative slopes and clusters with positive slopes increased with fish size (Table 2).

Bottom trawl survey

For pollock <20 cm, we observed a decrease in pollock biomass with temperature in cluster A3 covering the area west of the Pribilof Islands and north to Zhemchug Canyon (Fig. 3A). We observed an increase in pollock biomass in shallower areas north of Pribilof Island (A4), as well as in the areas of 50–100 m depth east from the Pribilof Islands (A5). The magnitude of change was somewhat smaller than that observed for the EITS survey (see Fig. 3A for details).

For pollock 20–29 cm, we observed a decrease in biomass from 70% to 5% in the area northwest of the Pribilof Islands (cluster B5). A cumulative increase in biomass from 7% to 52% of total biomass was observed in clusters B1 and B4 north of B5, and in clusters B6 and B7 in shallower waters (Fig. 3B). Relatively weak relationships were found between pollock biomass and temperature for clusters B2, B3, and B8.

For pollock 30–39 cm, we observed a temperature-related decrease in biomass in clusters C2 and C4 (42% to 1%, and 68% to 12% accordingly) (Fig. 2C). Increase in biomass was observed in cluster C1 (2–32%) north from C2. Positive change was also observed in cluster C5 (0–17%) within the shallow (<100 m) part of the southeastern Bering Sea shelf.

Clusters D2 and D4 represented areas where we observed a significant decrease in biomass for pollock 40–49 cm (from 5% to 1%, and from 41% to 11%) (Fig. 3D). Increased biomass was detected in cluster D1 located north from D4 and in D5 located to the east of D4 in shallower waters.

Very small changes were detected for pollock >50 cm. Although three clusters had a relatively strong pollock biomass and temperature relationship, the magnitude of biomass changes within the range of observed temperatures was quite small (Fig. 3E).

Overall, as with the EIT surveys, northward shifts in distribution in warmer years were found in the BT survey data for pollock <30 cm. The magnitude of these northward shifts was somewhat smaller (15–30%) than those detected by EIT surveys. In addition, these data suggested an inshore eastward redistribution of pollock in warmer years. Changes for pollock >50 cm were evident but small (in the range of 15%).

Discussion

Inferring seasonal pollock migration from interannual variations in distribution

Interannual differences in the timing of the migration from spawning grounds to forage areas are related to water temperatures. The relationship between temperature and the spatial distribution of a seasonally migrating species could represent either a change in the winter location of the stock or a change in the timing of the migration or both (Mountain and Murawski, 1992). Although the evidence is not conclusive, data suggest that most pollock populations spawn in late winter or early spring in the same locations year after year (Bailey et al., 1999a). For example, large, prespawning aggregations of pollock have been surveyed around

[3] Ianelli, J. N., T. Buckley, T. Honkalehto, N. Williamson, and G. Walters. 2001. Bering Sea-Aleutian Islands walleye pollock assessment for 2002. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions, p. 1–105. North Pac. Fish. Manag. Council, Anchorage, AK.

Bogoslof Island every year since 1988 in the winter (Honkalehto et al.[4]). Further support that temperature is related to the timing of the postspawning migration may come from temperature effects on physiological aspects of spawning. Cold water temperatures may delay the onset of spawning and extend the spawning period of walleye pollock as has been found for another gadid (Kjesbu, 1994) and for flatfish (Lange and Greve, 1997) in the Atlantic.

The surveyed distribution of pollock in warmer years should be more representative of that seen later in a typical spring-summer warming cycle than the distribution of pollock seen in colder years. Bottom temperatures generally increased over the EBS and northern Bering Sea (NBS) during spring and summer (Overland et al., 1999; Khen et al., 2001; Stabeno et al., 2001). Our results show that the warmer the bottom water during spring-summer groundfish surveys, the farther away pollock <50 cm are found from their major spawning grounds. Thus, we interpret areas having lower pollock density with increasing temperature (clusters with negative slope) to be areas from which pollock are emigrating, and areas having higher pollock density with increasing temperature (clusters with positive slope) to be areas to which pollock are immigrating (Figs. 2 and 3).

Routes and directions of the migrations

As the water warms during spring and summer, pollock generally migrate northward, northwestward, and inshore to shallower waters. Larger pollock (>30 cm) begin their feeding migration from spawning grounds. In many areas (white areas—Figs. 2 and 3) we did not detect a significant increase or decrease in pollock abundance in relation to temperature, e.g., in the major pollock spawning area north of Unimak Island (Hinckley, 1987; Bulatov, 1989), and this finding may indicate that migration progressed beyond this area before it was surveyed, even in the coldest years, or that migrations were not pronounced in this area. However, we observed a very large decrease in biomass with increasing temperature in the Pribilof Islands area (i.e., within clusters A3, B5, C4, D4, E2, H3, and I2), which is another important pollock spawning location (Maeda and Hirakawa, 1977; Hinckley, 1987; Bulatov, 1989; Bailey et al., 1999a). An offsetting increase in biomass was observed in the northernmost part of the survey area (clusters B1, C1, D1, F1, G1, H1, and I1) and in shallower waters (clusters A4, A5, B6, B7, C5, and D5), which may indicate that pollock migrate north and inshore during the warming season. Echo integration trawl data indicate that smaller pollock (<29 cm) probably begin their migration from overwintering areas (clusters F2 and G2) located mainly northwest of the Zhemchug Canyon. These results agree with observations made by Bailey et al. (1999b) that small age-0, age-1, and age-2 pollock are distributed farther north than larger age-3 and older pollock. Migrations continued generally northward to the U.S.-Russia Convention Line. The near-bottom part of the pollock population (detected in the BT survey) also migrates northeastward into shallower waters. At this point we cannot describe the exact starting and ending points of migration but only the general direction, because surveys are performed after most of the spawning has been completed, and we lacked data for the NBS, where part of the pollock EBS population is probably migrating.

The direction of movements indicated by the EIT survey data and the BT survey data were somewhat different because of the effect of depth on the availability of pollock to each survey. As pollock migrate into shallower water they become more available to the BT survey and less available to the EIT survey. Therefore the BT survey indicates greater movement into shallower water, whereas the EIT survey indicates greater movement in a northerly direction.

Seasonal migrations by pollock in the EBS are broadly recognized as occurring but have not been well substantiated; however, most of the general observations and descriptions are in agreement with our results. It is generally recognized that the feeding migration of some EBS pollock takes them northwestward beyond our survey area and into Russian waters (Shuntov et al., 1992; 1993; Stepanenko, 2001). Pola (1985), in her numerical simulation of pollock migrations in the EBS identified two types of pollock feeding migration. One was temperature induced in the northward direction, and the other was seasonal in the northeastern direction toward shallower waters. Shuntov et al. (1993) considered migrational activity to start with the onset of sexual maturity, but our findings indicate that immature pollock do undergo feeding migrations in a northwestward direction, but over shorter distances than those traveled by mature pollock. Stepanenko (2001) also recognized migration by immature pollock. Only a few pollock tagged in the EBS have been recovered (Yoshida, 1985), but the relationships between the release and recovery locations are consistent with our findings of a northwestward feeding migration during the spring and summer over most of the EBS shelf and a northeastward migration into shallower water on the southeast EBS shelf.

Length-based differences in migration patterns

Our analysis of the EIT surveys indicates that the migrations of pollock <30 cm are shorter than those of pollock 30–50 cm. The distance pollock need to cover from clusters F2 and G2 to clusters F1 and G1 (241.3 km and 217.5 km) is much shorter than the distance to be covered by larger fish from clusters H4, H3, H2,

[4] Honkalehto, T., N. Williamson, D. Hanson, D. McKelvey, and S. de Blois. 2002b. Results of the echo Integration-trawl survey of walleye pollock (*Theragra chalcograma*) conducted on the southeastern Bering Sea shelf and in the southeastern Aleutian Basin near Bogoslof Island in February and March 2002. AFSC Processed Report 2002-02, 49 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle, WA 98115.

and I2 to clusters H1 and I1 (368.3 km and 453.7 km, respectively). Similar size-dependent differences in the distance of seasonal migrations were reported for Pacific hake (*Merluccius productus*), another gadoid from the north Pacific (Dorn, 1995). These observations may support the length-based hypothesis of Nøttestad et al. (1999) for feeding migrations in pelagic fish. Focusing on the energetic cost-benefit relationship of long distance migration, they concluded that migration distance is a function of length, weight, and age. Smaller fish may undergo shorter feeding migrations because the energetic cost of migration can exceed their total energy intake resulting from the of greater hydrodynamic drag associated with smaller fish size.

Migrations of the largest pollock (>50 cm), detected from the BT survey data, were of much lower magnitude then those of smaller fish. Our models indicate that only about 15% of fish in this length category move between clusters in the northeastern direction toward shallower waters. These small changes detected in BT data contradict those seen in EIT data. Whereas a small northward shift in biomass (mostly from cluster E2 to cluster E4) was detected with BT data, a southeastward shift was detected with EIT data. However, because the EIT survey is not well suited for estimating the distribution of pollock >50 cm, we are inclined to put more weight on the BT data to explain temperature-related changes in biomass distribution for this length category. Larger pollock (>50 cm) appear to change their migratory behavior. Shuntov (1992) noticed that the distribution of larger pollock (>54 cm) fundamentally differs from that of smaller pollock and that larger pollock are more benthic in behavior and feeding. Stepanenko (2001) did not observe any migrations to the Russian zone for pollock six years or older. We propose that the difference in the migratory behavior between pollock <50 cm and pollock >50 cm is linked to a well-known shift toward a diet of fish with increasing pollock size (Bailey and Dunn, 1979; Dwyer et al., 1987).

Why do pollock migrate?

Pollock feeding migrations in the EBS may be driven by a combination of four factors: temperature, zooplankton production, currents, and length of daylight.

Changes in the water temperature may affect pollock migrations. Bottom water temperature over the Bering Sea shelf rises between April and September (Pavlov and Pavlov, 1996; Overland et al., 1999; Khen et al., 2001; Stabeno et al., 2001). Our results indicate that with rising temperature pollock generally migrate northward and inshore. Pollock appear to avoid temperatures below 0°C (Swartzman et al., 1994); therefore a seasonal increase in temperature above 0°C can open new geographic areas for migration. Temperature was presented as one of several important stimuli affecting fish movements by Harden Jones (1968) and by Wielgolaski (1990), who noticed that capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), and haddock (*Melanogrammus aeglefinus*) in the Barents Sea migrate north towards a preferred temperature, either directly to satisfy metabolic requirements, or indirectly, as when attracted by food organisms.

Seasonal patterns in zooplankton production and prey availability largely coincide with seasonal patterns in pollock migration and distribution. The role of food availability in driving fish-feeding migrations has been described for other zooplanktivores such as Pacific hake (Dorn, 1995), Atlantic herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*), mackerel (*Scomber scombrus*) and capelin (Nøttestad et al., 1999). In the Bering Sea, the abundance of zooplankton is high on the EBS and NBS shelf throughout spring and summer, but it remains high in autumn only in the NBS (Springer et al., 1989; Chuchukalo et al., 1996; Coyle et al., 1996). Copepods and euphausiids are major prey groups for pollock during spring and summer in the northwest area of the EBS shelf, but in autumn, 30–49 cm pollock increase their feeding on fish and decapods (Dwyer et al., 1987) which may be related to a decrease in the availability of these prey (Willette et al., 1999) in this area. Further north in the Navarin-Anadyr area, copepods and euphausiids remain major prey components in the diet of pollock <50 cm through summer and autumn (Shuntov et al., 2000). The migration pattern of pollock indicates they may follow their food supply as the production and abundance of zooplankton proceeds northward. Pollock larger than 50 cm do not undergo northward feeding migrations because small pollock, other fish, and benthos are the main components of the diet (Dwyer et al., 1987; Yoshida, 1994; Shuntov at al., 2000).

In the area of pollock migrations northwest of Pribilof Islands current speeds are in the range of 1–5 cm/s at the 100 m depth and they generally run in the northwest direction (Stabeno et al., 2001). Current direction coincides with the direction of pollock migrations, so that the cost of the migration may be offset by swimming in the same direction as the transporting current (Nøttestad et al., 1999). Water currents can also influence fish migration indirectly by providing visual stimuli arising from the moving background (Harden Jones, 1968) or by transporting food. Springer et al. (1989) suggested that the transport of zooplankton by the northwest current may cause greater levels of zooplankton concentration in the NBS. Because of the lack of data on current speed, he speculated that a current velocity in the range of 20 cm/s was needed to explain these high levels of zooplankton in the NBS if the high levels of zooplankton are based only on currents. The latest observations of current on the Bering Sea shelf do not support these hypotheses (Stabeno et al., 2001). However northwestern currents may contribute to higher zooplankton biomass in the NBS.

Nøttestad et al. (1999) suggested that light conditions may play a role in fish feeding migrations because during summer day-length increases the farther north fish travel, thus potentially increasing feeding duration for pelagic visual predators. Pollock are visual predators and light conditions affect feeding efficiency of pollock

(Ryer and Olla, 1999; Ryer et al., 2002); therefore it may be that longer days at northern latitudes make a northward feeding migration beneficial by possibly providing an extended window of search time if the pollock happen to be in a locally depauperate area. However, day-length remains long enough in the entire Bering Sea for pollock to feed to satiation, and their gastric evacuation rate is slow (Dwyer et al., 1987), making the need to entirely fill their stomachs every day very unlikely.

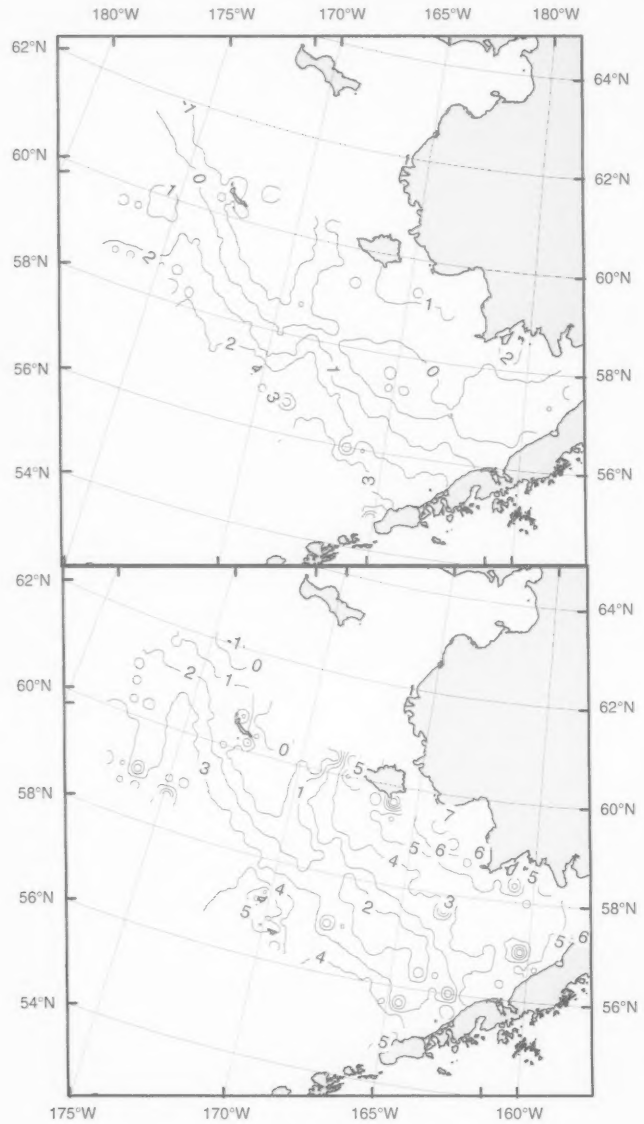

Figure 5

Bottom water temperature contours during the bottom trawl survey in the coldest year (1999—upper map) and warmest year (1996—lower map).

At this time it is impossible to assess which factor is most important in driving pollock migrations, but in summary we can conclude that pollock, as visual pelagic predators, benefit from northward feeding migrations during seasonal warming. Because three of the factors (excluding current) are similar throughout the Northern Hemisphere, we should see similar migration patterns for other pelagic fish of the north. Other examples include Pacific hake migrating along the North American west coast from California to British Columbia (Francis and Bailey, 1983; Dorn, 1995). Herring in the Norwegian Sea undergo seasonal feeding migrations in the northwestern direction from the south-central coast of Norway to the areas located northeast of Iceland (Ferno, 1998). Blue whiting, mackerel, and capelin from the north Atlantic undergo northward feeding migrations (Nøttestad et al., 1999). Pacific saury (*Cololabis saira*), chub mackerel (*Scomber japonicus*), Pacific sardine (*Sardinops sagax melanosticta*), and Japanese anchovy (*Engraulis japonicus*) from the western North Pacific are reported to migrate northwards during the summer (Novikov, 1986). Capelin, Atlantic cod, and haddock in the Barents Sea migrate north towards a "preference" temperature during summer (Wielgolaski, 1990). All these species have characteristics similar to those of Bering Sea pollock—that is, a pelagic or semipelagic life style, a diet of zooplankton, winter or spring spawning activity, and feeding migrations that take place during spring and summer.

Why is temperature important?

Temperature may affect the proportion of the stock that is in the standard EBS survey area. Ianelli et al.,[3] using population modeling, estimated that fewer pollock were detected during the BT survey in the EBS with increasing temperature, and fewer pollock would indicate that pollock are probably leaving the survey area during seasonal migrations. We conclude that a significant part of the EBS pollock population migrates into the Navarin-Anadyr area, which can have an impact on the way the EBS stock is managed. We should account for landings of pollock in the Navarin-Anadyr area, estimate how much of these landings include pollock from the EBS stock, and use this estimate in determining the EBS total allowable catch. Further research is needed to quantify the proportion of the EBS stock migrating into the Russian fishing zone and to estimate the number of pollock caught there. Stokes[5] suggested that the biomass estimates from the NBS are in the range of 0.5–1.0 million

[5] *See next page for footnote text.*

metric tons per annum and the exploitation rate is in the range of 0.5 million metric tons (50–100% of the total estimate).

Ongoing climate changes may affect pollock distribution between the U.S. and Russian EEZs. Stabeno and Overland (2001) reported a shift toward an earlier spring transition in the Bering Sea. This can affect the starting time of pollock migrations and the length of time fish spend in the Russian EEZ, increasing the availability of fish to the Russian fleet. This situation should encourage us to closely monitor changes in migration patterns of pollock in the Bering Sea.

Significant bias or error variation may be caused by the interaction of fish movement with survey protocol. For even relatively low fish migration velocities (<0.5 m/s), bias in estimated fish biomass can be very large (McAllister, 1998). Therefore, fish migration vectors should be estimated to minimize the bias created by not taking into account these migrations in biomass estimates.

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Toward identification of larval sailfish (*Istiophorus platypterus*), white marlin (*Tetrapturus albidus*), and blue marlin (*Makaira nigricans*) in the western North Atlantic Ocean*

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Abstract—The identification of larval istiophorid billfishes from the western North Atlantic Ocean has long been problematic. In the present study, a molecular technique was used to positively identify 27 larval white marlin (*Tetrapturus albidus*), 96 larval blue marlin (*Makaira nigricans*), and 591 larval sailfish (*Istiophorus platypterus*) from the Straits of Florida and the Bahamas. Nine morphometric measurements were taken for a subset of larvae (species known), and lower jaw pigment patterns were recorded on a grid. Canonical variates analysis (CVA) was used to reveal the extent to which the combination of morphometric, pigment pattern, and month of capture information was diagnostic to species level. Linear regression revealed species-specific relationships between the ratio of snout length to eye orbit diameter and standard length (SL). Confidence limits about these relationships served as defining characters for sailfish >10 mm SL and for blue and white marlin >17 mm SL. Pigment pattern analysis indicated that 40% of the preflexion blue marlin examined possessed a characteristic lower jaw pigment pattern and that 62% of sailfish larvae were identifiable by lower jaw pigments alone. An identification key was constructed based on pigment patterns, month of capture, and relationships between SL and the ratio of snout length to eye orbit diameter. The key yielded identifications for 69.4% of 304 (blind sample) larvae used to test it; only one of these identifications was incorrect. Of the 93 larvae that could not be identified by the key, 71 (76.3%) were correctly identified with CVA. Although identification of certain larval specimens may always require molecular techniques, it is encouraging that the majority (92.4%) of istiophorid larvae examined were ultimately identifiable from external characteristics alone.

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Fish. Bull. 103:588–600 (2005).

Research on the early life history of exploited fishes benefits management efforts by elucidating the temporal and spatial distribution of spawning, cohort strength, and biological and physical factors affecting recruitment (Lasker, 1987). The ability to confidently identify specimens to species is necessary in any early life history study (Collette and Vecchione, 1995). This has not yet been achieved for larval billfishes of the family Istiophoridae from the Atlantic Ocean: sailfish (*Istiophorus platypterus*), blue marlin (*Makaira nigricans*), white marlin (*Tetrapturus albidus*), and longbill spearfish (*Tetrapturus pfluegeri*).

Larval istiophorids are easily distinguished from larval swordfish (*Xiphias gladius*, family Xiphiidae). However, larval istiophorids are difficult to identify below the family level. Full fin-ray complements are not present until a larva reaches 20 mm in length, and even then, meristic counts are of limited use for identification because of significant overlap in counts among species. At best, species possibilities can be eliminated only for specimens with counts in the extremes of their ranges (Richards, 1974). The only definitively diagnostic count is the vertebral formula for *Makaira* (11 precaudal and 13 caudal) versus that of the other istiophorids (12 precaudal and 12 caudal) (Richards, 1974). Larger blue marlin lar-

* Contribution SFD-2003-0010 from NOAA Fisheries Sustainable Fisheries Division, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149.

vae may also be identified by the presence of a complex lateral line. Ueyanagi (1964) found this character in Pacific blue marlin of 20 mm standard length (SL), but the smallest SL of an Atlantic blue marlin from a recent collection in which a complex lateral line was visible was 26.9 mm. At lengths <20 mm, specific identification of istiophorids is even more uncertain. Ueyanagi (1963; 1964) based the identification of Indo-Pacific istiophorids <5 mm SL on four characters: 1) anterior projection of the eye orbit; 2) the position of the tip of the snout in relation to the middle of the eye; 3) presence of pigments on the branchiostegal and gular membranes; and 4) whether the pectoral fins are rigid—a character that applies to larval black marlin (*Makaira indica*), a species not known to spawn in the Atlantic Ocean. For fish >5 mm SL, the characters of relative snout length and eye size are used. Ueyanagi (1964) described sailfish, striped marlin (*Tetrapturus audax*, the Pacific counterpart to white marlin), and shortbill spearfish (*Tetrapturus angustirostris*) between 10 and 20 mm SL as having long snouts. The short snout group comprised blue marlin and black marlin. The angles at which the pterotic and preopercular spines protrude from the body have also been useful in identifying Indo-Pacific specimens (Ueyanagi, 1974a).

A troubling aspect of current larval istiophorid identification methods is the difficulty in using some of the above characters. If a specimen is fixed with its mouth open, snout position with respect to eye is an unreadable character (Richards, 1974), and misidentifications can occur (Ueyanagi, 1974a). Evaluation of certain characters (e.g., whether the eye orbit projects anteriorly) can be highly subjective. The lack of confirming identification characters compounds the problem; if just one character cannot be assessed, identification may not be possible (Richards, 1974). An additional problem is the apparently high variability in characters such as pigment locations and head spine angles in Atlantic istiophorids (Richards, 1974).

Most of the larval specimens examined by Ueyanagi came from the Indo-Pacific; he assumed that the same identification characters would apply to their Atlantic counterparts (Ueyanagi, 1963, 1974a). Although recent genetic evidence supports Morrow and Harbo's (1969) opinion that Atlantic and Indo-Pacific sailfish are actually populations of a global species (Finnerty and Block, 1995; Graves and McDowell, 1995), morphological differences have been noted in sailfish, especially at 90 cm. Specifically, the pectoral fin is longer, in relation to the body, in Atlantic sailfish than in Indo-Pacific sailfish. Differences in the spread of the caudal fin and maximum total length have also been observed. These characters were the impetus behind the separation of sailfish, at least to subspecies, by ocean basin (Nakamura, 1974). Regardless of the taxonomic status of the Atlantic and Indo-Pacific billfishes, physical attributes of istiophorid species may vary by region. Therefore, the assumption that the larvae of Atlantic istiophorids can be identified by using the same characters attributed to Indo-Pacific istiophorids may not be valid.

Billfishes are not the only group whose larval identification has proven difficult. Species of the genus *Sebastes*, the rockfishes, have some morphological and pigmentation differences as larvae, but identification was difficult and uncertain until genetic methods were employed (Rocha-Olivares et al., 2000). Fulford and Rutherford (2000) solved a similar problem by combining allozyme analysis of larval tissues with landmark-based morphometrics to distinguish between species of the genus *Morone*. In each study, a molecular technique was used to confirm larval species identity, facilitating the development of morphometric identification techniques.

Several molecular methods for identifying adult billfishes have been developed (Chow, 1993; Innes et al., 1998; McDowell and Graves, 2002). In the present study, larval istiophorids from Atlantic waters were identified to species using restriction fragment length polymorphism (RFLP) analysis of a 1.2-kb segment of nuclear DNA, as described for adult billfishes by McDowell and Graves (2002). In this article we present data for genetically identified istiophorid larvae, analyses of morphometric and qualitative characters, and a key for the identification of larval istiophorids of the Straits of Florida and the Bahamas.

Materials and methods

Larval material

Larval istiophorids were collected between June 1998 and April 2002 from the Straits of Florida and Exuma Sound, Bahamas. Several preservation fluids were used, but the majority of the larvae (~1000) were preserved in 70–95% ethanol. Butylated hydroxytoluene (BHT) saturated ethanol was used to preserve 150 larvae. Approximately 300 larvae were fixed in 10% unbuffered formalin and then transferred to 70% ethanol. In the laboratory, each fish was assigned a unique identification number and stored separately.

Molecular identification

Total DNA was extracted from the right eyeball of each larva, using either a quick-digest method (Ruzzante et al., 1996) or a standard high-molecular weight DNA extraction protocol (Sambrook et al., 1989). Larval identification was achieved by PCR amplification of the nuclear locus MN32-2 (Buonaccorsi et al., 1999), and subsequent RFLP analysis (restriction endonucleases *Dra* I and *Dde* I, Life Technologies, Bethesda, MD). If the restriction fragment pattern (Fig. 1) of a larva matched one of those described for a known-identity adult, the larva was assigned to that species. See McDowell and Graves (2002) for detailed protocols and reaction parameters. Preliminary attempts to amplify DNA from formalin-fixed larvae failed; only ethanol-preserved specimens were used in subsequent molecular work.

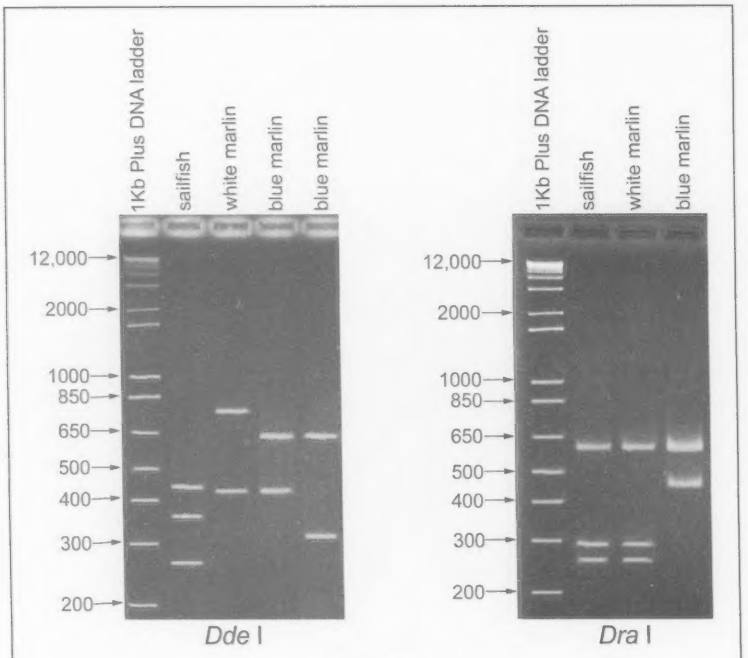

Figure 1

Common *Dde* I and *Dra* I restriction patterns for the MN32-2 locus of positively identified larval istiophorids from the Straits of Florida and the Bahamas. The left lane of each gel contains a DNA size standard (Life Technologies, Bethesda, MD), measured in base pairs.

Characters

A subset of the molecularly identified istiophorid larvae were examined to ascertain which morphological characters might aid in specific identification and possibly obviate the need for future molecular work. The measurements made by Richards (1974) served as a starting point for quantitative larval descriptions: standard length (SL); snout length (SN); tip of the snout to the center of the eyeball (SN-E); diameter of the eye (ED); diameter of the eye orbit (OD); head length (HL); and difference in length between the upper and lower jaws (JD). To this suite were added measurements of the preopercular (PRO) and pterotic (PTS) head spines. All measurements were taken with Image-Pro Plus software (version 4.5, Media Cybernetics, Silver Spring, MD), and each specimen was viewed through a CoolSNAP-PROcf monochrome digital camera (Media Cybernetics, Silver Spring, MD) which was connected to a Leica MZ12 dissecting microscope (at magnifications 0.8–10.0×). Each larva was soaked in tap water for one minute before measurements were taken, to rehydrate the fish and facilitate handling. SL and PRO measurements were made from the dorsal view, JD measurements were made from the ventral view, and all other measurements were made from the left lateral view (Fig. 2). Because the preopercular spine often prevents an istiophorid larva from lying on its side, a side view was obtained by using the surface tension of the still-wet larva to adhere it to the side wall of a Petri dish. Care was taken to maintain the two points of measurement on a plane parallel to the microscope lens.

Pigments observed on the ventral surface of the lower jaw rami, gular membrane, and branchiostegal membranes of each larva were drawn onto a generalized diagram of the larval istiophorid lower jaw (Fig. 3). A grid was then superimposed on the diagram, and the shape (pointate or stellate) and number of chromatophores in each grid cell were recorded. Pigment data were also recorded as binary presence or absence per grid cell. Two other categorical variables assessed were flexion stage (i.e., preflexion, flexing, postflexion) and the position of the tip of the snout with regard to a plane passing through the center of the eye and the mid-line of the body (i.e., below, even, above). Although the latter character is useful for identifying Indo-Pacific istiophorids (Ueyanagi, 1963, 1964), in our collection it was highly variable within species, and therefore it was not analyzed further.

Month of capture was considered a partially discriminating character based on differences in the length and timing of spawning seasons of local populations. Spawning seasons were determined by de Sylva and Breder (1997) by gonad histology studies.

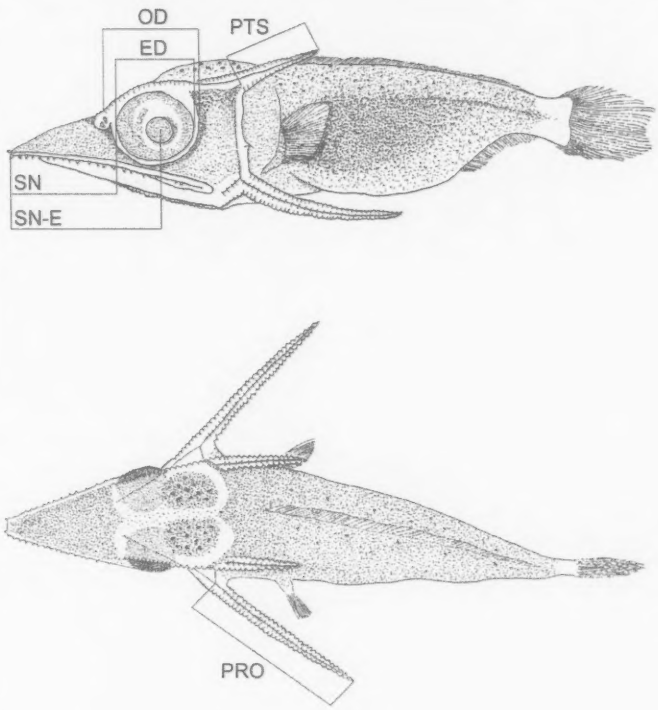

Figure 2

Morphometric measurements illustrated on a 10.7-mm SL sailfish. SN = snout length; SN-E = snout to mid-eye; OD = eye orbit diameter; ED = eye diameter; PTS = length of pterotic spine; PRO = length of preopercular spine. Drawings by S. Luthy.

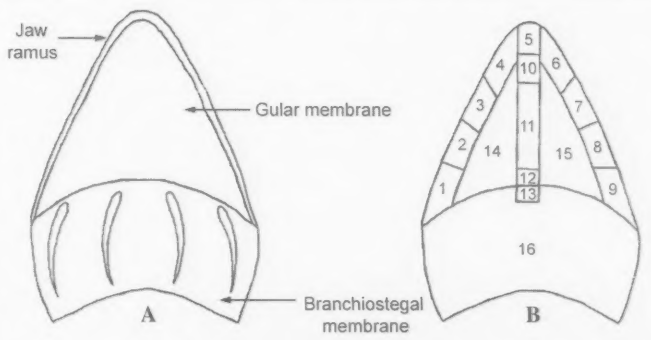

Figure 3

Lower jaw pigments were characterized by drawing chromatophores onto a generalized lower jaw diagram (**A**), reproduced from Richards (1974). A grid (**B**) was then superimposed onto the diagram and the number and shape of chromatophores were recorded for each grid cell. The numbers in diagram B are numbers used to identify the cells of the grid and not the number of chromatophores per cell.

Data analyses

Canonical variates analysis (CVA) was used to visualize the separation between species and the relative importance of all variables (morphometric characters, pigment patterns, and month of capture) in that separation. Results from the CVA were used to help drive character selection for subsequent analyses. The significance of the canonical axes was obtained with a Monte Carlo permutation test (499 iterations). The canonical analyses were performed with the software CANOCO (version 4.5, Microcomputer Power, Ithaca, NY), and plotted with the associated software CANODRAW.

In the CVA, all the molecularly identified white marlin (21) and blue marlin (68) with full measurement sets (i.e., no missing values) and a subset of sailfish (135) with full measurement sets were compared. Every attempt was made to include fish from different locations, different years and months of collection, and across the full available size range of each species, in order to capture as much intra- and inter-species variation as possible. Forward selection was used as a guide for the creation of a reduced set of variables by retaining those that were significant for discrimination at α=0.05 in a Monte Carlo permutation test (499 iterations). Months that were excluded by selection were restored to the variable set to insure that the entire spawning season was represented. It was assumed that pigment on the right lower jaw ramus was of equal importance as pigment in the corresponding location on the left lower jaw ramus; thus if a pigment grid from only one side of the jaw was selected, the corresponding grid from the other side of the jaw was added back to the reduced set.

In addition to its function as an exploratory tool for character selection, CVA with the reduced set of variables was used to identify unknown larvae to species. Ordination coordinates of an unknown larva were obtained by summing the products of the canonical coefficients and the character values for the unknown (standardized to mean 0, standard deviation 1). The identity of an unknown larva was determined by its placement in the ordination with respect to the reference larvae.

The CVA provided clues as to which individual pigment grid cells were important for species discrimination, but cluster analysis was employed to examine overall lower jaw pigment patterns. Simple average link cluster analysis of Jaccard similarity indices was executed on pigment grid cell presence (binary coding) in the suite of lower jaw grid cells with BioDiversity Pro[1] software for the 26 white marlin with undamaged lower jaws and for equal numbers of randomly chosen blue marlin and sailfish. Analyses were conducted on all larvae together, and separately by flexion stage. Pigment drawings of the individual larvae within single-species clusters were examined visually for commonalities. If a pattern was detected, the entire database of pigment position, number, and shape of all molecularly identified larvae was searched for that pattern. Lower jaw pigment patterns that were confined to one species only were deemed diagnostic characters.

Lower jaw pigment patterns alone did not resolve the differences among the species sufficiently for identification of all larvae. Therefore, for each species, continuous variables related linearly to SL were regressed against SL by using SAS (version 8.02, SAS Institute, Cary, NC) software. Two ratios were also examined in this way—snout length divided by eye orbit diameter, and snout length divided by eye diameter. Both ratios were suggested by the results of the full-model CVA because the influence of snout length was large and opposite in sign to the large and similar vectors of orbit diameter and eye diameter. The former ratio was also considered by Ueyanagi (1963, 1964, 1974b) to be an important distinguishing character for istiophorid larvae. The same larvae that were used in the CVA analyses were used for the regressions, plus three white marlin, two sailfish, and two blue marlin that were excluded from CVA because of a missing measurement. Suitability of the characters for linear regression was assessed visually. Confidence intervals of 95%, 99%, and 99.9% were constructed around the regressions. Intersections of the three levels of confidence intervals for the three species were examined for maximum discrimination at the smallest standard length. The relationships that provided the best separation were included in the identification key.

The identification key was constructed from the various characters that showed differences among the three species. All of the larvae used in developing the key were tested with it, as well as 12 blue marlin and 61 sailfish that were previously excluded from the analyses. A set of 50 larvae were independently identified by two observers unfamiliar with the key (naïve observers). The only information about the fish provided to them was month of capture, so that each made his own measurements and pigment evaluations. The percent accuracy of their identifications was taken as a measure of the utility of the key.

Results

Molecular identification

The molecular identification technique was applied to 1044 larvae. Amplification success rates appear to have been negatively affected by the addition of BHT to ethanol and by the use of the Ruzzante et al. (1996) DNA extraction protocol. Overall, 714 (68.4%) istiophorids were successfully identified to the species level. Sailfish represented 82.8% of this group (591 larvae), whereas 96 blue marlin (13.4%) and 27 white marlin (3.8%) were identified. No longbill spearfish were identified. Sailfish larvae (2.9 mm–18.3 mm SL) were collected from April

[1] McAleece, N., P. J. D. Lambshead, G. L. J. Paterson, and J. D. Gage. 1997. The National History Museum and The Scottish Association for Marine Science. Website: http://www.sams.ac.uk/. [Accessed 5 February 2003.]

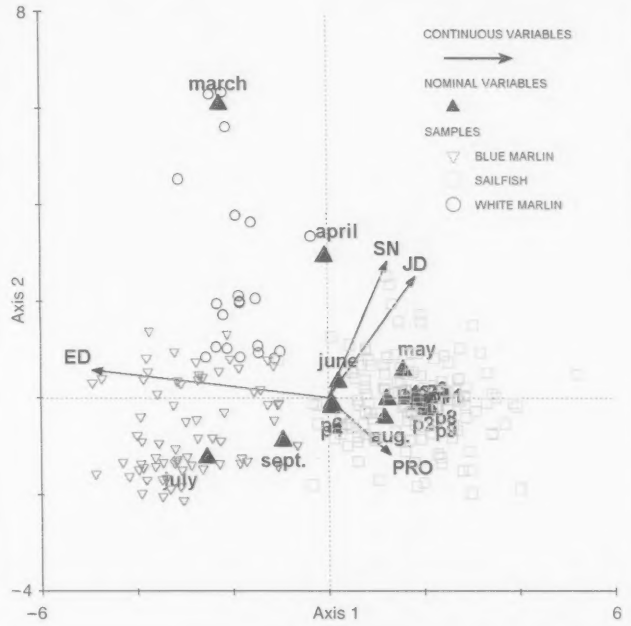

Figure 4

Canonical variates analysis with the reduced set of variables. Arrows indicate the direction of increase in continuous variables and may be extended backward through the origin of the graph to show a decrease in the value of the character. Variables that extend farthest from the origin are most useful in the separation. SN = snout length; JD = difference in the lengths of the jaws; ED = eye diameter; PRO = length of preopercular spine; p (number) = presence of pigment in lower jaw grid cell (number).

through September, white marlin (4.5 mm–20.3 mm SL) were collected from March through June, and larval blue marlin (3.8 mm–22.1 mm SL) were collected from June through September. Month of capture closely matched the reported spawning seasons for these species in the western North Atlantic: April through October for sailfish, March through June for white marlin, and July through October for blue marlin (de Sylva and Breder, 1997). Because blue marlin larvae were also caught in June, the blue marlin spawning season was expanded to include that month for the purposes of the identification key.

Canonical variates analysis

In the CVA with all variables included, separation of the three species was achieved with little overlap. Sailfish larvae were separated from the marlins along canonical axis 1 (eigenvalue=5.45). The separation was driven mainly by ED, OD, and lower jaw pigmentation. White marlin larvae separated from blue marlin primarily along canonical axis 2 (eigenvalue=0.79), largely by month of capture, as well as SN, SN–E, and JD . The overall ordination was significant at P=0.002.

The forward selection process, along with the re-addition of counterpart pigment grids and the full spawning season, yielded the following 21 out of 32 variables: March, April, May, June, July, August, September, SN, JD, ED, PRO, and pigment grids 1–4, 6–9, 11, and 12. The following variables were ultimately excluded from the data set: SL, SN-E, OD, HL, PTS, and pigment grids 5, 10, and 13–16. The degree of species overlap was similar to that in the full model (Fig. 4). This overall ordination was also significant at P=0.002. The eigenvalue of the first canonical axis was 4.71, whereas the eigenvalue of the second canonical axis was 0.71. Coordinates obtained from the canonical coefficients and character values, standardized by reference set character means and standard deviations (Table 1), accurately placed test "unknowns" in the ordination of the reference larvae.

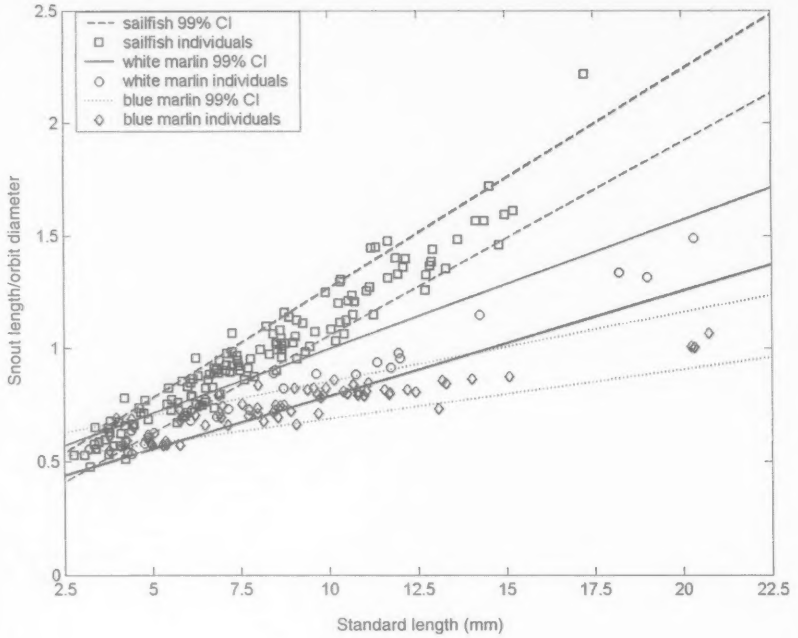

Figure 5

Relationship of the ratio of snout length to orbit diameter with standard length. Lines represent 99% confidence intervals.

Lower jaw pigment patterns

Sailfish of all flexion stages with chromatophores on one or both sides of the lower jaw rami and sometimes in the middle of the gular membrane comprised single-species clusters. Examination of all molecularly identified larvae showed that many sailfish had pigment on the posterior ¾ of the lower jaw, but a few marlins also had stray pigments in that region. The minimum criterion to identify sailfish by lower jaw pigment without misidentifying other species was pigment in at least three of lower jaw pigment grids 1, 2, 3, 7, 8, 9, and 11. The shape and number of chromatophores within the grids was inconsequential. Not all sailfish larvae possessed the putative sailfish pattern, but 61.8% of molecularly identified sailfish (353 of 571 with intact lower jaws) could be identified by their lower jaw pigments alone.

Preflexion and flexing blue marlin also formed single-species clusters owing to the pattern of a single, pointate chromatophore in each of lower jaw grid cells 4 and 6, but without any other pigment (except occasionally in grid cell 12 or 13). However, not all small blue marlin exhibited this pattern. Eight of the 20 (40%) preflexion, molecularly identified blue marlin with intact lower jaws could be accurately identified by lower jaw pigments. Although some postflexion white marlin had a similar pattern, no preflexion or flexing larvae of other species were misidentified as blue marlin by virtue of this pigment pattern.

Linear regressions

Residual plots showed no deviations from homogeneity of variance. Snout length, snout to mid-eye, ratio of snout length to eye diameter, and ratio of snout length to orbit diameter were all linearly related to SL. Jaw difference was linear and appeared to be helpful for discriminating istiophorids >12 mm SL, but too few larvae of this size were available for meaningful regressions. The ratio of snout length to orbit diameter provided the most separation between the species as indicated by the full model CVA. The 99% upper limit of the regression of this ratio against SL for white marlin was used to separate sailfish from both marlin species at 10 mm SL. If white marlin is ruled out as a possibility by month of capture, sailfish can be separated from blue marlin by the blue marlin upper 99% confidence limit for the regression of the ratio of snout length to orbit diameter at 8 mm SL. The lower 99% confidence limit for the regression of the ratio of white marlin snout length to orbit diameter separated them from blue marlin at 17 mm SL (Fig. 5, Table 2).

Table 1

Canonical coefficients, mean, and standard deviation of each character from the canonical variates analysis (reduced set of characters). The coordinate of a larva on canonical axis 1 (x) can be found by $x=\sum_{i=1}^{21} c_{1i} z_i$, where c = canonical coefficient and z = (character value − character mean)/character standard deviation. The coordinate of a larva on canonical axis 2 (y) can be found by $x=\sum_{i=1}^{21} c_{2i} z_i$. PRO = pre-opercular; SN = snout length; ED = eye diameter; and JD = difference in length between upper and lower jaws.

i (iterative count)	Character	Canonical coefficient, c_1, for canonical axis 1	Canonical coefficient, c_2, for canonical axis 2	Character mean (reference set)	Character standard deviation (reference set)
1	March	−0.0963	0.7538	0.0134	0.1149
2	April	0.0772	0.7354	0.0357	0.1856
3	May	0.1961	0.7347	0.1786	0.3830
4	June	0.1267	0.6460	0.3036	0.4598
5	July	−0.0369	−0.2988	0.2054	0.4040
6	August	0.3465	0.2116	0.2143	0.4103
7	September	0.0000	0.0000	0.0491	0.2161
8	PRO	0.6697	−0.6728	2.0781	0.7076
9	SN	3.1678	0.9640	1.4978	0.8711
10	ED	−2.8386	0.0739	1.2011	0.4426
11	JD	−0.9464	−0.4947	0.1806	0.2222
12	Pigment 1	0.1450	−0.1156	0.2366	0.4250
13	Pigment 2	0.3483	−0.0953	0.2366	0.4250
14	Pigment 3	0.3564	0.1262	0.3036	0.4598
15	Pigment 4	0.0887	−0.2251	0.7768	0.4164
16	Pigment 6	−0.0263	−0.1084	0.8214	0.3830
17	Pigment 7	−0.0375	−0.1584	0.3259	0.4687
18	Pigment 8	0.2684	−0.0507	0.2098	0.4072
19	Pigment 9	0.3262	−0.0603	0.2545	0.4356
20	Pigment 11	0.4757	−0.1622	0.4241	0.4942
21	Pigment 12	0.2250	−0.1191	0.3438	0.4750

Table 2

Regression of the ratio of snout length to orbit diameter against standard length. r^2 = coefficient of determination and n = number of fish in sample.

Species	Regression equation	r^2	n
Sailfish (*Istiophorus platypterus*)	$SN{:}OD = 0.092SL + 0.242$	0.94	137
White marlin (*Tetrapturus albidus*)	$SN{:}OD = 0.052SL + 0.373$	0.95	24
Blue marlin (*Makaira nigricans*)	$SN{:}OD = 0.026SL + 0.510$	0.74	70

Identification methods

Combination of species diagnostic lower jaw pigment patterns, regression equations, and month of capture resulted in the identification key found in Table 3. Of the 304 larvae that were examined with the key by the authors, only one was misidentified. This was an 8.02-mm blue marlin that was mistakenly identified as a sailfish by question 6a in part I of the key. Of the remaining fish, 31 larvae, all between 4 mm and 10 mm SL could not be identified with the key. An additional 62 larvae, again mostly less than 10 mm SL, could be narrowed down to only two species possibilities. Overall, 69.1% of the fish were correctly identified to species. Accuracy improved with size. Eighty-five of the 93 larvae that could not be identified by the key were plotted as unknowns on the ordination (reduced set of variables), at which time correct identification was obtained for 71 of them. Seven larvae could not be identified at all, and seven were incorrectly identified because they were plotted at the interface of two species groupings. The remaining eight were incompatible with CVA because

Table 3

Key for ethanol-preserved larvae and postlarval specimens of Istiophoridae caught in the Straits of Florida and the Bahamas.

Part I: for larvae <10 mm standard length (SL)

1a Preflexion or flexing; a single, pointate chromatophore in each of lower jaw pigment grids 4 and 6; with or without a single pigment in either grid 12 or 13; no other lower jaw pigments ..... ***Makaira nigricans***

1b Not as above **2**

2a Any flexion stage; chromatophores of any number or shape in 3 or more of lower jaw pigment grids 1, 2, 3, 7, 8, 9, 11 ..... ***Istiophorus platypterus***

2b Not as above **3**

3a Larva caught in March, April, or May ..... either ***Istiophorus platypterus*** or ***Tetrapturus albidus***

3b Larva caught in June or later **4**

4a Larva caught in June ..... either ***Istiophorus platypterus***, ***Tetrapturus albidus***, or ***Makaira nigricans***

4b Larva caught in July, August, September, or October **5**

5a Standard length ≥8 mm **6**

5b Standard length <8 mm ..... either ***Istiophorus platypterus*** or ***Makaira nigricans***

6a Snout length / orbit diameter >0.030*SL* + 0.551 ..... ***Istiophorus platypterus***

6b Snout length / orbit diameter ≤0.030*SL* + 0.551 ..... ***Makaira nigricans***

Part II: for larvae ≥10 mm SL

1a Chromatophores of any number or shape in 3 or more of lower jaw pigment grids 1, 2, 3, 7, 8, 9, 11 ..... ***Istiophorus platypterus***

1b Without the above lower jaw pigment pattern **2**

2a Snout length / orbit diameter >0.057*SL* + 0.427 ..... ***Istiophorus platypterus***

2b Snout length / orbit diameter ≤0.057*SL* + 0.427 ..... **3**

3a Larva caught in March, April, or May ..... ***Tetrapturus albidus***

3b Larva caught in June or later **4**

4a Larva caught in July, August, September, or October ..... ***Makaira nigricans***

4b Larva caught in June **5**

5a Standard length ≥17 mm **6**

5b Standard length <17 mm ..... either ***Makaira nigricans*** or ***Tetrapturus albidus***

6a Snout length / orbit diameter ≥0.047*SL* + 0.319 ..... ***Tetrapturus albidus***

6b Snout length / orbit diameter <0.047*SL* + 0.319 ..... ***Makaira nigricans***

a measurement was missing. Thus, when the key and CVA analyses were combined, 92.4% of the tested larvae were correctly identified.

One of the two naïve observers found that one larva out of the test set of 50 was too damaged to be evaluated. He correctly identified 35 larvae and found 14 to be unidentifiable with the key. Overall, his success rate was 71.4%. The other observer correctly identified 30 larvae, misidentified one (the larva not evaluated by the other observer and the same larva misidentified by the authors), and found 19 to be unidentifiable by the key. His overall success rate was 60%. The difference in the number of larvae that could not be identified with the key was the result of differences in interpretation of the lower jaw pigment position for larvae less than 10 mm SL.

Discussion

Because adults of four istiophorid species are found in the Straits of Florida and Bahamian waters, a reliable larval identification technique for these species is necessary (Voss, 1953). Incorrect species identifications can have serious ramifications on other areas of istiophorid early life history research. For example, studies on early growth would suffer if a larval blue marlin, which is thought to reach 174 cm lower jaw fork length (LJFL) by age one (Prince et al., 1991), were to be confused with a larval sailfish, which reportedly grows to only 108.9 cm LJFL (Hedgepeth and Jolley, 1983; Prager et al., 1995) by age one.

Few characters are available to separate the species of larval istiophorids (Richards, 1974). Although

a single character may be used to separate fish into groups, early work has lacked a means to confirm the identity of the groups. Molecular techniques provided a solution to this problem. A limitation of the molecular identification technique that we used was that only those larvae preserved in ethanol could be identified. Formalin fixation does not always preclude the use of PCR-based methods, but work is usually limited to small fragments; 570 bp is considered large for successful amplification (Shedlock et al., 1997). In the present study, DNA quality was too low in the formalin-fixed istiophorid larvae for PCR to amplify the 1.2-kb MN32-2. Consequently, only ethanol-preserved larvae could be used for key development and testing. Because of likely differences in length shrinkage between larvae preserved only in ethanol and those fixed in formalin, it is possible that the regressions presented in the present study are not valid for the latter.

No longbill spearfish were among the molecularly identified larvae; thus this species could not be included in the key. Very little is known about the longbill spearfish, but it is reported that larvae are found offshore (Ueyanagi et al., 1970), and that even adults are quite rare in United States and Bahamian waters (Robins, 1975). The longbill spearfish spawning season appears to range from late November to early May and peaks in February (Robins, 1975; de Sylva and Breder, 1997). Although there is some overlap in the spawning season of longbill spearfish with the spawning seasons of other Atlantic istiophorids, because of the rarity and predominantly offshore occurrence of the longbill spearfish, its absence from the key may not pose major problems for the identification of istiophorid larvae from our study area.

The larval istiophorids used to create and test the identification key were all captured either in the Straits of Florida or in Bahamian waters and were all smaller than 22 mm SL. Caution must be used when applying the key to larvae from other parts of the world or to larger sizes. Ueyanagi (1963) assumed that species pairs from different oceans (white marlin and striped marlin [*Tetrapturus audax*], longbill spearfish and shortbill spearfish [*Tetrapturus angustirostris*], Atlantic and Pacific blue marlin, Atlantic and Pacific sailfish]) would be identifiable by the same characters. Although these pairs exhibit the same RFLP patterns at the MN32-2 locus (McDowell and Graves, 2002), we have not tested the key with Pacific larvae and cannot be certain that their measurements would fall within the same regression limits or that they would have the same lower jaw pigment patterns. Even within the Atlantic Ocean, spawning seasons vary with location (e.g., Bartlett and Haedrich [1968] collected larval blue marlin off the coast of Brazil in February and March). Month of capture was crucial in our analyses for discriminating between small marlins when spawning season overlap is minimal; therefore our key may need adjustment to reflect local spawning seasons when applied to other locations.

As in Indo-Pacific istiophorid larvae (Ueyanagi, 1964, 1974b), snout length, eye orbit diameter, and lower jaw pigmentation are important characters for identifying larval istiophorids of the western Atlantic. However, white marlin differ markedly from their Indo-Pacific counterpart, striped marlin. White marlin larvae, long-held as members of the "long-snout group" of istiophorids, actually more closely resemble the short-snouted blue marlin until 17 mm standard length (Fig. 6). After they reach this size, snout length is intermediate between that of blue marlin and sailfish. This result cautions against the assumption that even large larvae with short snouts are blue marlin. Snout length may be useful as a character in phylogeny studies.

The identification methods presented in the present study reduce subjectivity in the evaluation of characters. This study also brings to light the caveats of using lower jaw pigment patterns as a means of identification and limits which pigment patterns qualify as diagnostic. Although there is a family of lower jaw pigment patterns that appears to mark sailfish only, if this character were the only means of identifying sailfish, nearly 40% of our sailfish (as confirmed by RFLP analysis) would have been misidentified or escaped classification. Likewise, the preflexion blue marlin pigment pattern will not lead to misidentifications, but too many preflexion blue marlin lack the pattern to justify its use as a stand-alone identification character. Lower jaw pigment patterns have also been suggested as potentially useful characters for separation of subspecific populations of both sailfish (Ueyanagi, 1974a, 1974b) and striped marlin in the Indo-Pacific (Nishikawa, 1991). The hypothesis of pigment-delineated sailfish populations was not borne out (Leis et al., 1987), and the high variability of lower jaw pigments among larvae of each species from our study area casts further doubt on the notion of using pigments alone to distinguish populations.

Our identification key does not enable separation of species for certain classes of istiophorid larvae. For example, larvae that are caught in June, are less than 10 mm SL, and possess none of the diagnostic lower jaw pigment patterns are especially problematic. In these "dead end" cases, discriminant analysis (CVA) is useful. Although a few larvae were misidentified with the CVA, these larvae were plotted near the interface of two species groupings; this position alerts the user to the fact that misidentification is a possibility. One disadvantage of using CVA (or any discriminant analysis) for identification is that all of the variables must have a value, meaning that a larva with broken preopercular spines, for example, cannot be entered into the analysis. When the species possibilities are narrowed down to blue marlin and either sailfish or white marlin, it may be feasible to identify larvae by vertebral formula. Richards (1974) suggests that this is difficult with larvae less than 20 mm SL, but it is the method that Prince et al. (1991) used to identify blue marlin that were 5–10 mm SL. Molecular identification is always an option for resolving dead ends.

The identification of larval istiophorids has never been an easy task. Molecular identification is reliable, but can be relatively more labor intensive and expensive

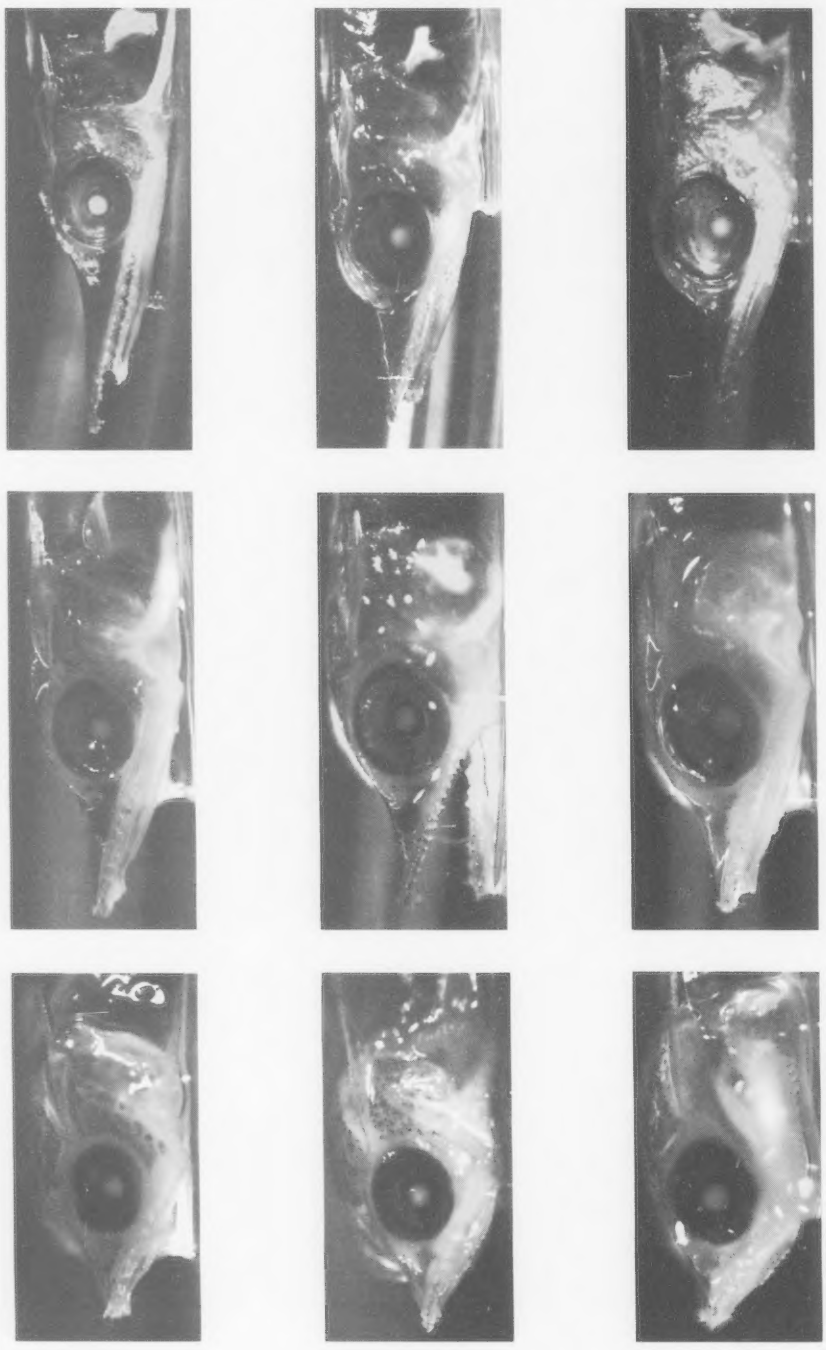

Figure 6

Size series of genetically identified representatives of each species. Top row: sailfish. Middle row: white marlin. Bottom row: blue marlin. Left column: ~5 mm SL. Middle column: ~10 mm SL. Right column: ~15 mm SL.

than traditional methods. The creation of a key based on characters developed from molecularly identified Atlantic larvae makes it possible to use more traditional methods to make reliable identifications. Despite the limitations of the key, it works well for larvae caught in our area. We recommend further testing with istiophorid larvae from other waters, and the inclusion of longbill spearfish larvae.

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Sexual differentiation and gonad development in striped mullet (*Mugil cephalus* L.) from South Carolina estuaries*

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Abstract—This study examined the sexual differentiation and reproductive dynamics of striped mullet (*Mugil cephalus* L.) in the estuaries of South Carolina. A total of 16,464 specimens were captured during the study and histological examination of sex and maturity was performed on a subsample of 3670 fish. Striped mullet were sexually undifferentiated for the first 12 months, began differentiation at 13 months, and were 90% fully differentiated by 15 to 19 months of age and 225 mm total length (TL). The defining morphological characteristics for differentiating males was the elongation of the protogonial germ tissue in a corradiating pattern towards the center of the lobe, the development of primary and secondary ducts, and the lack of any recognizable ovarian wall structure. The defining female characteristics were the formation of protogonial germ tissue into spherical germ cell nests, separation of a tissue layer from the outer epithelial layer of the lobe-forming ovarian walls, a tissue bud growing from the suspensory tissue that helped form the ovary wall, and the proliferation of oogonia and oocytes. Sexual maturation in male striped mullet first occurred at 1 year and 248 mm TL and 100% maturity occurred at age 2 and 300 mm TL. Female striped mullet first matured at 2 years and 291 mm total length and 100% maturity occurred at 400 mm TL and age 4. Because of the open ocean spawning behavior of striped mullet, all stages of maturity were observed in males and females except for functionally mature females with hydrated oocytes. The spawning season for striped mullet recruiting to South Carolina estuaries lasts from October to April; the majority of spawning activity, however, occurs from November to January. Ovarian atresia was observed to have four distinct phases. This study presents morphological analysis of reproductive ontogeny in relation to size and age in South Carolina striped mullet. Because of the length of the undifferentiated gonad stage in juvenile striped mullet, previous studies have proposed the possibility of protandric hermaphrodism in this species. The results of our study indicate that striped mullet are gonochoristic but capable of exhibiting nonfunctional hermaphroditic characteristics in differentiated mature gonads.

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The striped mullet (*Mugil cephalus* L.) is distributed circumglobally in tropical and semitropical waters between latitudes 42°N and 42°S (Thomson, 1963; Rossi et al., 1998). Even though considered a marine species, striped mullet are euryhaline and can be found year round throughout the full range of estuarine salinities in the southeastern United States (Jacot, 1920; Anderson, 1958). Striped mullet are important throughout the world for commercial fisheries and aquaculture. In the southeastern United States there are large-scale commercial fisheries for striped mullet in North Carolina and Florida. South Carolina and Georgia have much more limited landings (NMFS[1]).

The commercial effort in the southeastern United States targets "roe" fish (fish containing roe) during the fall spawning migration. Throughout the rest of the year mullet are fished commercially for human consumption (particularly the west coast of Florida) and bait (Anderson, 1958). Striped mullet have a significant economic impact in the southeast where they represented a landings value of 16.4 million dollars from 1994 to 2000 (NMFS[1]). Striped mullet landings in the Gulf of Mexico were significantly higher with a landings value of 86.2 million dollars for the same time period. Striped mullet are also one of the most important forage fishes that occur in the estuaries of the southeast and represent a significant food source for upper level piscivores (Wenner et al.[2]).

General information on the biology of striped mullet has been well documented (Jacot, 1920; Anderson, 1958; Thomson, 1963, 1966; Chubb et al., 1981) but limited information is available on the reproductive biology of wild populations (Anderson, 1958; Stenger, 1959; Greeley et al., 1987; Render et al., 1995). There is a large body of work concerning striped mullet reproduction in aquaculture but many of these studies have concentrated on females by using artificial manipulation of the reproductive cycle. Although the maturation process of oocytes may be the same as that in wild striped mullet, the environment and conditions under which maturation occurred in these studies was artificial (Shehadeh et al., 1973; Kuo et al., 1974; Pien and Liao, 1975, Kelly, 1990; Tamaru et al., 1994; Kuo, 1995). This lack of in-

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[1] NMFS (National Marine Fisheries Service). 2001. Unpubl. data. Statistics and Economic Division, 1315 East-West Highway, Silver Spring, Md. 20910. http://www.st.nmfs.gov/st1/index.html.

[2] Wenner, C. A., W. A. Roumillat, J. E. Moran, M. B. Maddox, L. B. Daniel, and J. W. Smith. 1990. Investigations on the life history and population dynamics of marine recreational fishes in South Carolina, part 1, p. 2–22. Completion reports, Project F-37, Charleston, and Project F-31, Brunswick. South Carolina Marine Resources Research Institute, P.O. Box 12559 Charleston, S.C. 29422.

formation on reproductive biology is surprising given the worldwide importance of mullet. In particular, there have been very few studies where sexual differentiation of immature striped mullet has been examined in conjunction with histological confirmation of maturity stage in reproductively capable adults. One notable exception was the work of Stenger (1959), who although thorough in histological confirmation of the male and female developmental stages in relation to length, did not take age into consideration at differentiation or maturity. More recent studies (Chang et al., 1995; Chang et al., 1999) have examined gonad histology and plasma sex steroids during sex differentiation in young-of-the-year striped mullet up to 12 months old, but these studies did not provide any detail on fish length during development and differentiation. Other studies have examined oocyte development and relative fecundity for the reproductive assessment of female striped mullet but did not examine reproductive development in males or take into consideration an independent confirmation of fish age (Greeley et al., 1987; Render et al., 1995). Few studies have described the process of spermatogenesis in striped mullet because most efforts on the propagation and enhancement of striped mullet reproduction have concentrated on female development because of their commercial value. Grier (1981) used striped mullet in describing the cellular organization of testes and spermatogenesis as a model for synchronously spawning fishes but did not describe size and age in relation to spermatogenesis.

Striped mullet are considered isochronal spawning fishes (Greeley et al., 1987; Render et al., 1995). There are only a few observations of offshore spawning activity (Arnold and Thompson, 1958), and eggs and larvae have rarely been collected offshore (Anderson, 1958; Finucane et al., 1978; Collins and Stender, 1989). Collins and Stender (1989) concluded that striped mullet spawn in and around the edge of the continental shelf off the coasts of North Carolina, South Carolina, Georgia, and the east coast of Florida (an area often referred to as the South Atlantic Bight), but may also spawn outside the South Atlantic Bight (SAB). They also indicated a protracted spawning season that extended from October to April. This contrasts with the estimated spawning season from previous studies (2–5 months from November through March) (Jacot, 1920; Broadhead, 1956; Anderson, 1958; Arnold and Thompson, 1958; Stenger, 1959; Dindo and MacGregor, 1981; Greeley et al., 1987; Render et al., 1995; Hettler et al., 1997). Female mullet were thought to mature at three years of age at a size of 230 to 350 mm standard length (Thomson, 1951, 1963; Greeley et al., 1987).

This study had three purposes: 1) to determine at what size and age striped mullet become fully sexually differentiated and to describe the morphological characteristics of sexual differentiation in both male and female striped mullet; 2) to determine the size and age at first maturity for each sex; and 3) to describe the timing and process of gametogenesis in relation to size and age in both males and females in order to provide a histological baseline for the evaluation and reproductive staging of striped mullet.

Materials and methods

Sampling and data collection

Collections of striped mullet were conducted from October 1997 through December 2000. Collections were based on a protocol of monthly random stratified sampling conducted in the Cape Romain, Charleston Harbor, and the ACE Basin estuaries in South Carolina (Fig. 1). The Charleston Harbor estuarine system is made up of three river systems: the Ashley, Cooper, and Wando rivers. In addition, Charleston Harbor proper was sampled as a separate stratum. The ACE Basin estuary is formed by the confluence of the Ashepoo, Combahee, and Edisto rivers and was sampled as a single estuary. One of the problems initially encountered with sampling was the ability to sample striped mullet throughout their estuarine salinity range. The primary sampling gear used was a 184-meter trammel net with 356-mm stretch mesh outside panels and a 64-mm stretch mesh inner panel. Because striped mullet use the full range of estuarine habitats and freshwater, the use of alternate gear was necessary to obtain a representative sample of the population within all salinity regimes. Specimens collected with additional gear types in low salinity and freshwater habitats supplemented those specimens sampled with a trammel net. The additional gear types were an electroshock boat, cast nets, and gill nets. The electroshock boat samples were obtained from the South Carolina Department of Health and Environmental Control from the major coastal river basins in South Carolina, including freshwater portions of the Waccamaw, Black, Pee Dee, Sampit, Santee, Cooper, Edisto, Ashepoo, Combahee, and Broad rivers (Fig. 1). Cast nets were used primarily in different portions of the Charleston Harbor estuary in tidal creeks and in areas where the trammel net could not be used effectively . The cast nets were 1.84 meters in diameter and had 10-mm mesh. The gill net was a 200-meter net with 64-mm stretch mesh that was used to test the efficiency of the trammel net sets.

Standard morphological measurements were total length (TL), fork length (FL), standard length (SL) in mm, and body weight (BW) in grams (g). Any subsequent mention of fish length in the remaining text will be total length unless otherwise noted. Sagittal otoliths were removed for estimating fish ages. A gross examination of the gonads was used for initial sex and maturity assessment. If the gonads were estimated to weigh more than 1 g they were also weighed. A small sample of gonad tissue was removed from the posterior portion of the gonad where the lobes were joined and was fixed in 10% neutral buffered formalin for histological examination. The tissue samples used for histological evaluation were taken from the posterior section of the gonad because earlier developmental stages and differentiation were more evident where the ductwork

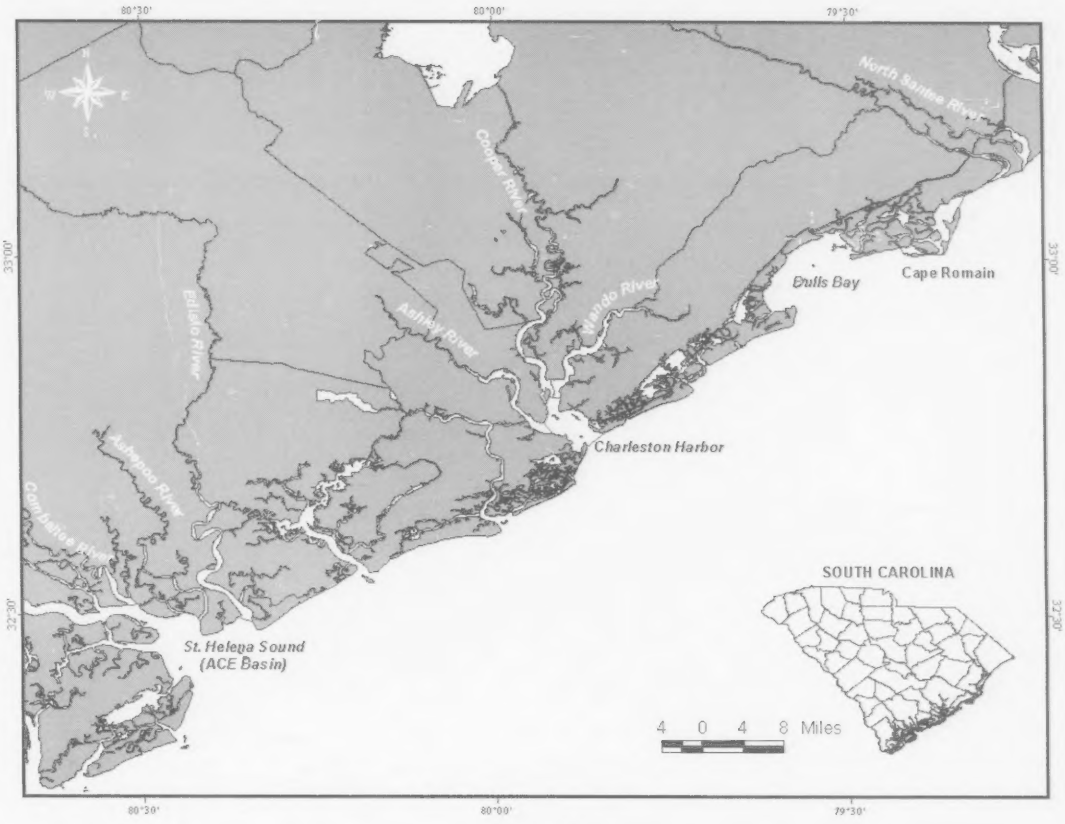


Figure 1

Map of coastal South Carolina with estuaries where trammel net collections were made: Cape Romain, Charleston Harbor, and Ashepoo River, Combahee River, Edisto River (ACE) Basin, as well as the coastal rivers where electroshock collections were made.

and gonad tissue joined in striped mullet (Chang et al., 1995). Comparisons of oocyte density from different sections of striped mullet ovary have also demonstrated uniform distribution throughout the ovary (Shehedeh et al., 1973; McDonough et al., 2003). A gonadosomatic index (GSI) was calculated for specimens according to the method of Render et al. (1995) where GSI was expressed as a percentage of gonad weight (GW) divided by body weight (BW) minus gonad weight, such that

$$GSI = (GW/(BW - GW)) \times 100.$$

Histological processing

The tissue samples were processed by using standard wax histology techniques (Humason, 1967). Tissues were embedded in paraffin and cut on a rotary microtome. The sections, which ranged from 5 to 7 μm thick, were then placed on microscope slides and stained with standard haematoxylin and eosin-Y staining techniques (Humason, 1967). After staining, tissue sections were sealed under a cover slip and evaluated for sex and maturity with a compound light microscope at 100× magnification. The sex of each specimen was determined to be male, female, or undifferentiated. Maturity was assessed according to a modified version of the schedule used by Wenner et al. (1986) that was adapted by the authors to work with isochronal spawning fish, as well as assessed with previous models of reproductive development (Stenger, 1959; Grier, 1981; Wallace and Selman, 1981) (Table 1). Ovarian atresia was divided into four distinct phases as described by Hunter and Macewicz (1985). For the sake of consistency, the same terminology was used to describe the four phases of ovarian atresia in striped mullet in this study: alpha, beta, gamma, and delta (see Table 2). These evaluation methods were based on identification of morphological characteristics evident in histological sections. Specimens were evaluated by two readers to avoid bias. Any discrepancies of maturity stage between readers were either mutually resolved or the specimen was excluded from further analysis.

Table 1

Histological criteria used to determine reproductive stage in striped mullet (*Mugil cephalus*) once sexual differentiation has occurred. Modified from Wenner et al. (1986).

Reproductive stage	Male	Female
1. Immature	Inactive testes; small transverse sections compared to those of resting male; spermatagonia and little or no spermatocytic development.	Inactive ovary with previtellogenic oocytes and no evidence of atresia. Oocytes are <80 μm, lamellae lack muscle, and connective tissue bundles are not as elongate as those in mature ovaries, ovary wall is very thin.
2. Developing	Development of cysts containing primary and secondary spermatocytes all the way through accumulation of spermatozoa in lobular lumina and ducts.	Developing ovary have enlarged oocytes generally greater than 120 μm in size. Cortical alveoli become present and actual vitellogenesis occurs after oocytes reach 180 μm in size and continue to increase in size. Abundant yolk globules with oocytes reach a size range of >600 μm,
3. Running, ripe	Predominance of spermatozoa in lobules and ducts and little occurrence of spermatogenesis.	Completion of yolk coalescence and hydration in most oocytes.
4. Atretic or spent	No spermatogenesis occurring but some residual spermatozoa in shrunken lobules and ducts.	More than 30% of developed oocytes undergoing the atretic process. See Table 2 for detailed description of the atretic process.
5. Inactive or resting	Larger transverse sections compared to those of immature males; little or no spermatocytic development; empty lobules with well-developed secondary ductwork and some residual spermatagonia.	Previtellogenic oocytes with only traces of atresia. In comparison to those of immature females, most oocytes are >80 μm, lamellae have some muscle and connective tissue bundles; lamellae are larger and more elongated than those of immature females and the ovarian wall is thicker.

Table 2

Histological criteria used to determine atretic stage in striped mullet (*Mugil cephalus*). Criteria based on ovarian atretic process described by Hunter and Macewicz (1985) and observational data of striped mullet ovaries from this study.

Atretic stage		Description
1. Alpha atresia	α	Vitellogenic oocytes are present with distinct yolk globules, which are beginning to break down. The most developmentally advanced oocytes will undergo atresia first, followed by less developed oocytes. The oocyte will break down from the interior outward; the vitelline membrane and follicle layers are the last portion of the oocyte to decay. As the oocyte breaks down, a series of vacuoles of various sizes will appear within the oocyte.
2. Beta atresia	β	The oocytes continue to become reduced in size as they decay. The vacuoles that began to form during the alpha stage are now coalescing together to form one large vacuole within the oocyte. This gives the lamellae a distinct hollow matrix and just the outer layers of the oocyte and follicle are now left. This appears to be the shortest atretic phase.
3. Gamma atresia	γ	The oocytes that were left in the hollow matrix during the beta stage now begin to shrink in size and the outer layers fold in on themselves as the oocyte collapses. The areas in and around the collapsed oocytes and lamellae become highly vascularized during this stage in order to facilitate rapid resorption of decaying cellular material. There will still be some vacuoles present within the collapsed oocytes but they have become much smaller and there are far fewer of them. This stage continues until most of the remaining oocytes that developed for spawning are no longer recognizable as oocytes.
4. Delta atresia	Δ	The remnants of old oocytes at this stage are identifiable only as decaying cellular material and will stain a distinct yellow-brown color and are still present in (approximately) 30% or more of the material within the ovary. Undeveloped oocytes have a much more distinct and numerous presence within individual lamellae. The amount of vascularization seen in the gamma stage is reduced because most of the old material has been reabsorbed.

Aging techniques

Age was determined by using the left sagittal otolith, which was embedded in epoxy resin. A 0.5-mm transverse section encompassing the otolith core was cut with an Isomet low speed saw with diamond wafering blades. The thin section of otolith embedded in the epoxy was observed with a dissection microscope at 20× magnification, and age was recorded as the number of annular rings present. The otoliths were initially aged by one reader. A second reader then evaluated a subsample of specimens from 1998 and 2000 and all the otoliths from 1999. The two groups of ages were compared by the percentage of agreement between the different age determinations and by a paired t-test that allowed a comparison of the means and variances of the two groups (Campana et al., 1995). Ages were then validated by marginal increment analysis in order to establish the timing and periodicity of increment deposition (Campana, 2001). In addition, the precision of the ages was compared by using average percent error (APE) between the two sets of ages. "Precision" was defined as the reproducibility of age determinations (Beamish and Fournier, 1981; Chang, 1982). Using the Levenburg-Marquardt procedure (Zar, 1984), we determined the growth curve with a nonlinear least squares regression of total length on age.

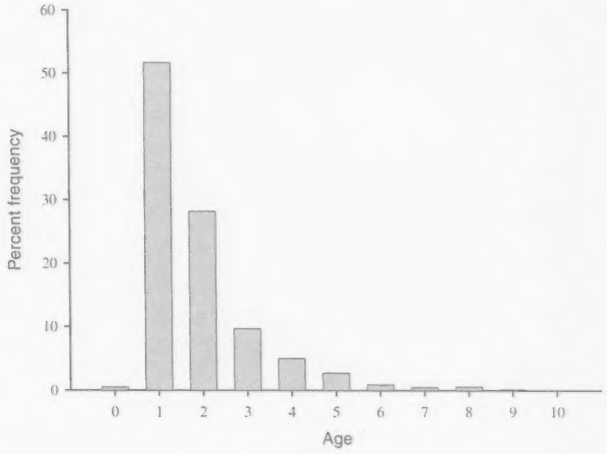


Figure 2

Age-frequency distribution (expressed as a percentage) for striped mullet (*Mugil cephalus* L.) from South Carolina estuaries October 1997 to December 2000. n=3760.

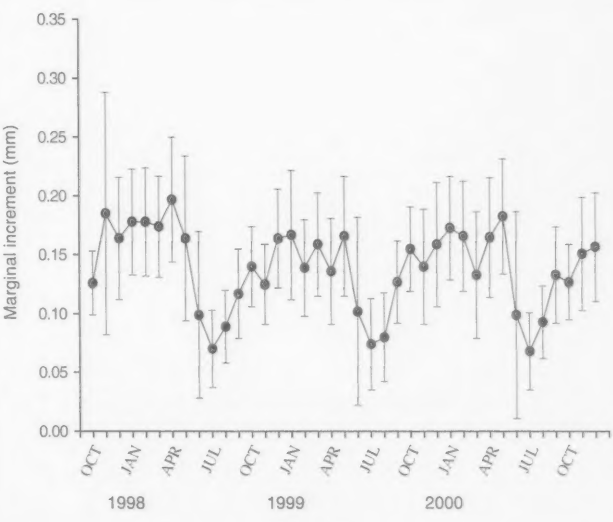


Figure 3

Mean marginal increment distance by month for striped mullet (*Mugil cephalus* L.) from South Carolina estuaries, October 1997 to December 2000. n=3760. Marginal increment equals the otolith section radius minus the distance from the core to the last annular increment.

Results

Age structure

We recorded the age of 3760 specimens and examined these specimens histologically to determine sex and maturity stage. An additional 2524 young-of-the-year (age 0) specimens were used for the nonlinear regression of total length on age, as well as the sex ratios by both size and age. The age range for striped mullet in this study was 0 to 10 years, and 1- and 2-year-olds dominated the age distribution (Fig. 2). There was 81.7% agreement for age data between the two readers, and 99.5% agreement within one year for both readers. A t-test indicated no significant difference between the two sets of age estimations (t=2.898, df=1,233, P<0.05). The average percent error (APE) (Beamish and Fournier, 1981) between the two sets of age estimations was 0.41%.

Marginal increment analysis indicated that growth increments were deposited during July (Fig. 3). The total length at age regression demonstrated a strong relationship (r^2=0.864, df=3759, F_{stat}=21,742, P<0.05). Despite this strong relationship, there was a wide range of sizes among the 1-, 2-, and 3-year-olds (Fig. 4).

There was a lag period between the time of formation of the first annual growth mark and the actual one-year birthdate. The first annular mark was deposited between 15 and 19 months of age or at 1.25 to 1.6 years of age (Wenner and McDonough[3]).

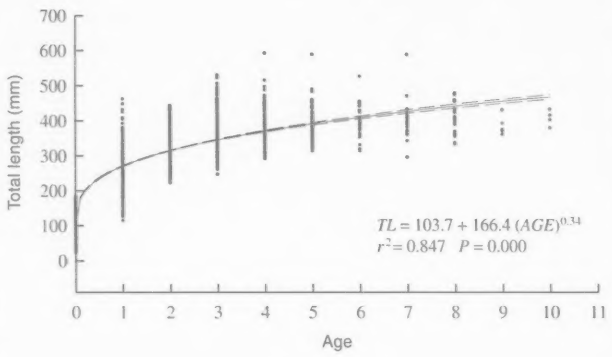


Figure 4

Nonlinear regression of total length on age for striped mullet (*Mugil cephalus* L.) from South Carolina estuaries, October 1997 to December 2000. n=6284.

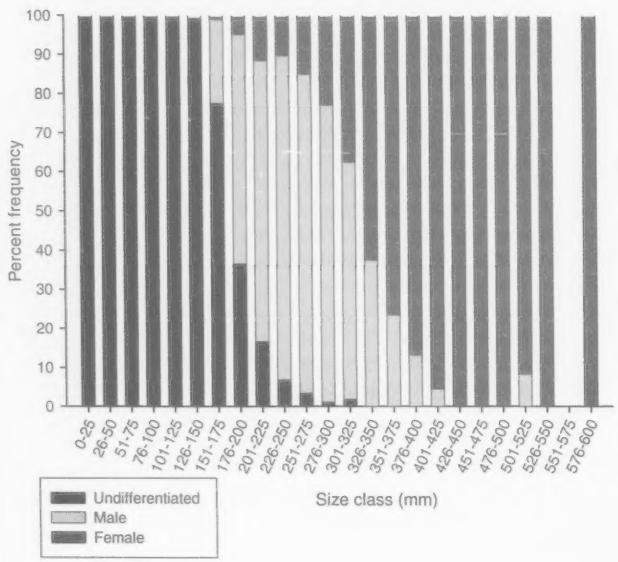


Figure 5

Sex by size class (25-mm size classes) for striped mullet (*Mugil cephalus* L.) from South Carolina estuaries, October 1997 to December 2000. n=6284.

Sexual differentiation

The smallest sexually differentiated male was 137 mm (Fig. 5). Male striped mullet 126 to 150 mm TL were eight to twelve months old (McDonough and Wenner, 2003). The first sexually differentiated female was 164 mm TL. Females 151 to 175 mm would have been approximately one year old (McDonough and Wenner, 2003). Specimens greater than 200 mm were at least 50% sexually differentiated. Only 1.5% of specimens over 300 mm remained undifferentiated. The largest sexually undifferentiated specimen was 325 mm. All fish >325 mm, although still possibly sexually immature, were fully sexually differentiated. The ratio of males to females was 2:1 until the fish were larger than 325 mm ($\chi^2_{\alpha=0.05}$=2543.9, df=2). The ratio of males to females was 1:3.8 for fish >325 mm ($\chi^2_{\alpha=0.05}$=352.8, df=1).

The sex ratio by age class showed 98.9% of the age-0 specimens were sexually undifferentiated (Fig. 6). The few age-0 fish that were differentiated were all males. At first annulus deposition, 91.9% of the specimens had differentiated. There were a few specimens (0.8%) that remained undifferentiated to 3 years old, but all striped mullet age 4 or older were completely differentiated. The sex ratio of males to females in the one-year-old age class was 1.0:0.25 ($\chi^2_{\alpha=0.05}$=1065.4, df=2). At age 2 the ratio was 1.0:0.68 ($\chi^2_{\alpha=0.05}$ =502.6, df=2) and at age 3 the ratio had reversed to 0.32:1.0 ($\chi^2_{\alpha=0.05}$=312.5, df=2).

Size and age at maturity

The onset of spermatogenesis in males was first observed at 248 mm (Fig. 7A). The first running, ripe males occurred at 291 mm and this developmental stage was found in all larger sizes. Postspawning males were found only between November and March in mullets larger than 325 mm. Resting mature males were found in every month and occurred in most size classes greater than 251 mm. These resting males made up fewer than 50% of the specimens from any particular size class. A small percent-

[3] Wenner, C. A., and C. J. McDonough. 2001. Cooperative research on the biology and assessment of nearshore and estuarine fishes along the southeast coast of the U.S.: Part IV: Striped mullet, *Mugil cephalus*, p. 17–23. Final Report, Grant no. NA77FF0550. Marine Resources Research Institute, South Carolina Dep. Natural Resources, P.O. Box 12559 Charleston, SC 29422-2559.

age (2.5%) of immature males were found in size classes greater than 325 mm. Male striped mullet showed 50% maturity at 275 mm, and 100% maturity by 350 mm.

Oogenesis began in specimens as small as 291 mm (Fig. 7B) and there were 15 females below 325 mm undergoing oogenesis (4.5% of all developing females). Ovaries were found in three small females (<300 mm). Immature females were not found larger than 400 mm or older than 3 years. All females greater than 400 mm were mature, regardless of their age. The majority of females over 425 mm (88.3%) were developing and found only in the fall. No ripe female striped mullet were found. Ovarian atresia was found from December through May. Female striped mullet showed that 50% maturity was reached at 325 mm, and 100% maturity occurred in specimens 400 mm.

Gametogenesis occurred in each sex between the first and second year (Fig. 8). However, the majority of specimens at age 1 (65%) were immature. Males and females showed 50% maturity at 2 years. Males showed 100% maturity at age 4 and females at age 5. Running, ripe males were first observed at age 1 but were found in much greater numbers at ages 4–6. Resting males occurred in every age class except age 6 (Fig. 8A). The abundance of males aged 3 and older was far lower (by at least an order of magnitude) than that of 1- and 2-year-olds (Fig. 8A). Atretic ovaries were found in all age classes, and resting females were found in every age class except age 0 (Fig. 8B).

Maturity stages by month showed immature and resting (but sexually mature) male and female striped mullet occurred in every month (Fig. 9). Developing males were found from August through February, and running, ripe males from October through February. Males (atretic) were found from November through March. Developing females occurred from August through April. Mean monthly GSI for males and females showed noticeably increased gonad size in November and December, and obviously enlarged gonads occurred from October through March (Fig. 10).

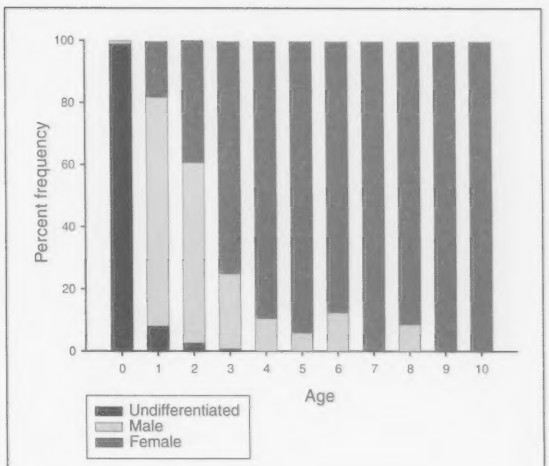


Figure 6

Sex by age class in years. Age is the number of annuli present on the sagittal otoliths. n=6284.

Histological descriptions: undifferentiated juveniles

The primordial gonad lobes were suspended by mesentery connected dorsally to the peritoneum and were attached ventrally to the intestines (Fig. 11A). Gonads from specimens <100 mm were identifiable only through histological examination of whole-body cross sections.

The gonads in specimens less than 50 mm had lobes ranging from 70 to 100 μm in length (Fig. 11B). Lobes were made up of somatic cells and a peripheral germinal epithelium. The lobes were attached along their dorsomedial surface by loose fibrous connective tissue, known as stromal tissue. No defining male or female characteristics were present at this fish length.

In specimens ranging from 50 to 100 μm gonad lobes had increased to 150 µm and appeared more vascularized (Fig. 11C). The lobes were attached to the suspensory mesentery, which was attached to the peritoneum. A few deuterogonia were visible along the lateral periphery of each lobe. The remainder of the lobes contained somatic tissue. The individual germ cells were approximately 5 μm in size. In some specimens, somatic tissue was beginning to form bands that would later develop into ductwork.

In specimens ranging from 100 to 150 mm, the gonad lobes were obviously vascularized and had attained a size of 200 to 300 µm (Fig. 11D). Early ductwork was beginning to become evident. Deuterogonia were enlarging and forming nests along the lateral and distal portions of the lobes. Somatic cells made up a large portion of each lobe and the stromal tissue was now more stalklike, attaching each lobe to the suspensory tissue. There were only four specimens in this size range that had started to differentiate as males. Gonads destined to be males were identified by duct structures within the gonad lobe as well as by more elongated germ cell nests. These morphologically distinct features resulted in an early demonstration of the corradiating pattern of ducts and lobules seen in more advanced testes.

The 150 to 200 mm size class showed that 0.2% of females and 37.3% of males began initial differentiation, but the majority of all specimens (62.5%) remained undifferentiated. The undifferentiated gonads had become larger, and lobe size was 600 to 800 µm (Fig. 11E). There was increased vascularization, particularly along the medial portion of the stroma. Germ-cell nests were now more organized, with 4 to 8 cells visible in each.

More than 83% of specimens >200 mm had become sexually differentiated. The undifferentiated gonads in specimens >200 mm were highly vascularized and had both the presence of ductwork, rounded germ cell nests, and lobule-like structures. In some cases, germ cell nests that were characteristic of female precursors

could also be found in the center portions of lobes adjacent to the characteristic male precursor lobule structures. The primary duct was now well formed; however there were still no definitive morphological characterstic that would enable sex determination.

Male differentiation

The initial differentiation of males was evident in the morphological features of the germ-cell tissue located along the peripheral portions of each lobe. The germ tissue began to form elongated bands perpendicular to the edge of the lobe, whereas the somatic tissue began to form fibrous bands originating along the edges of the primary duct (Fig. 12A). The primary duct was defined structurally at this point. With continued increase in fish length, lobes increased in size and vascularization. The germ tissue continued to elongate medially within the lobe in a corradiating pattern (Fig. 12B). Somatic tissue continued to form bandlike structures that would eventually become secondary ductwork, and the germ-cell expanded to form lobules (Fig. 12C). As the lobules became more developed, spermatogonia began to line the lobules as part of the germinal epithelium (Fig. 12D). Sertoli cells were not visible because of the lack of resolution at this magnification (400×) level. Mitotic proliferation of spermatogonia caused lobular enlargement, a;though spermatogonia were very small at this stage (2–3 μm). The overall male aspects of the physical structure of the lobes was clear at this point (Fig. 12E). Melanomacrophages were found in the lobes of some specimens (Fig. 12F). The melanomacrophages were found only in immature and differentiating males.

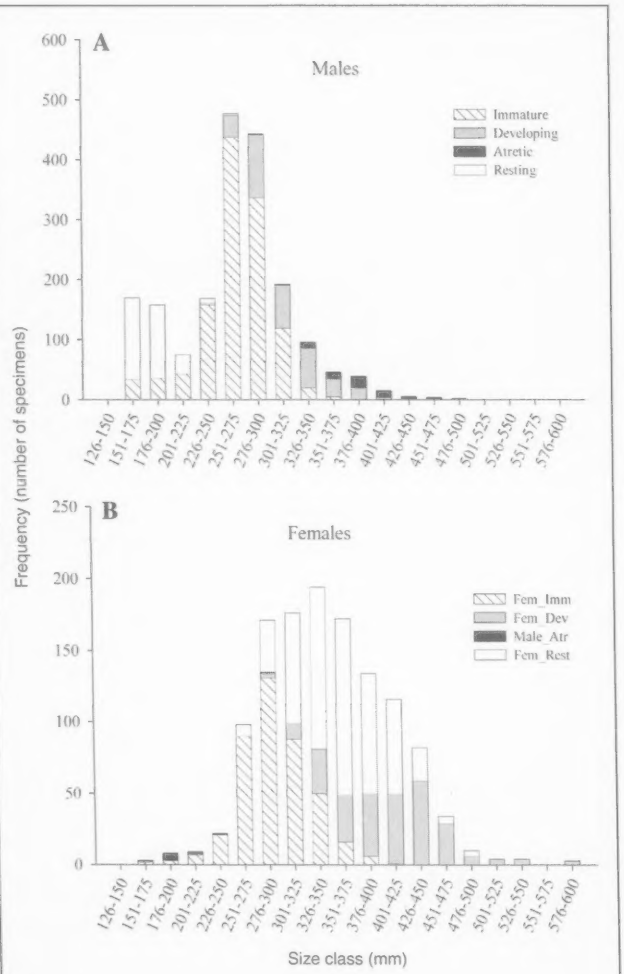


Figure 7

Maturity stage by size class for male and female striped mullet (*Mugil cephalus* L.) from South Carolina estuaries, October 1997 to December 2000. Males, n=1850; females, n=1250.

Female differentiation

The first sign of female sexual differentiation was the organization of germ-cell tissue into round nests of 8–10 cells each (Fig. 13A). The germ-cell nests, which eventually gave rise to oogonial nests, were first found along the lateral periphery of the lobe and were infrequently scattered within the gonad lobe. There was evidence of early ovarian wall development, which consisted of a single layer of cells forming the outer layer of the lobe, separate from the oogonial nests (Fig. 13B). Although some ductwork was present, there was no evidence of the formation of lamellae. Ductwork tended to become reduced as the germ-cell nests became more numerous. With continued development, individual cells within the nests became more visible and the ovary wall became more evident (Fig. 13B). Stalks or buds of tissue were observed growing out of the base of the stroma on the dorsolateral surface (Fig. 13C). As development progressed, the ovarian wall attached to these stalks or tissue buds appeared to grow over the dorsal surface of each ovarian lobe. This ovary-wall stalk bud was not necessarily an indicator of female differentiation because a small number of samples (0.6%) with definite male structure also had indications of these stalk buds. However, these tissue stalks were present in 68% of the differentiating females. The presence of both the ovary wall stalk buds and the rounded germ-cell nests located throughout the gonad lobe were diagnostic of female differentiation.

Primary growth oocytes increased in number and began to aggregate, forming distinct lamellae (Fig. 13D). The ovary wall continued to differentiate at this point but was only a few

cell layers thick. There was still a great deal of stroma and somatic tissue left in the ovary, but it began to form bands of fibrous tissue, resulting from the regression of stroma and somatic tissue (where present) as the lamellae continued to develop. The primary duct was greatly reduced. Oogonia began proliferating and differentiating into primary growth oocytes as folliculogenesis commenced. The ovary wall, now becoming vascularized, began to separate from the lamellae, opening a space that would become the ovarian lumen (Fig. 13, D–F). The ovary wall was made up of squamous cells on the inside layers and collagen and elastic tissue on the outer layers. The stroma and somatic cells continued to be reduced until they were primarily fibrous tissue from which the lamellae were suspended. Histological ovarian cross-sections changed from the leaf or spade shape of the undifferentiated gonad to a more rounded one. Once ovarian differentiation was completed, the individual lamellae were seen to have oocytes within each and the stroma was reduced to suspensory tissue for the lamellae (Fig. 13F). The primary growth oocytes present in the lamellae remained small (80 to 100 µm) and relatively uniform in size. At the initiation of reproductive development, the oocytes started to grow from the arrested prophase of the first meiotic division (Stenger, 1959; Kuo et al., 1974).

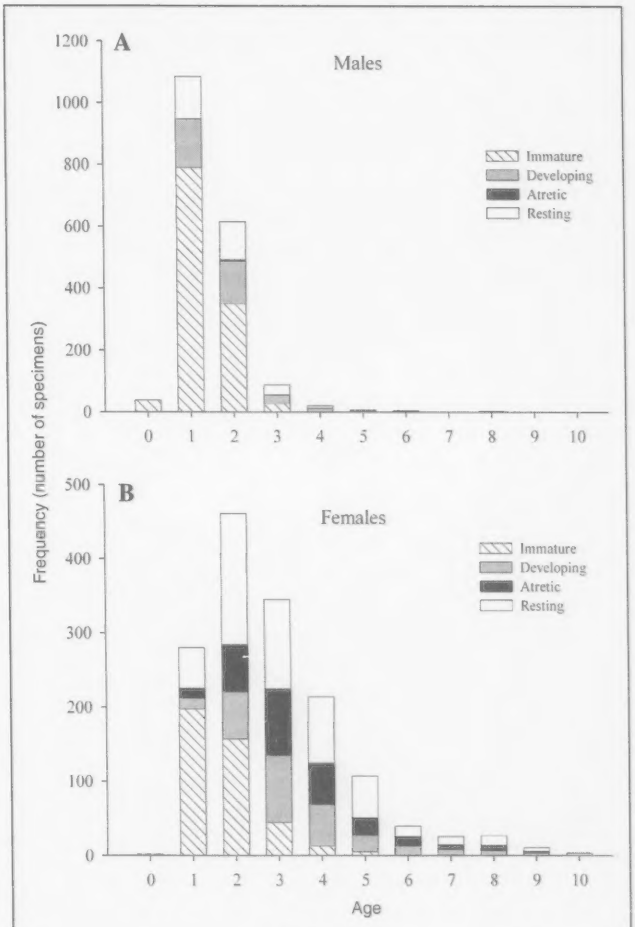


Figure 8

Maturity stage, by age class, for male and female striped mullet (*Mugil cephalus* L.)from South Carolina estuaries, October 1997 to December 2000. Males, n=1850; females, n=1250.

Morphological features of atretic females

Females undergoing atresia were captured in all months except August–October, and 78% were seen January–March of each year. The first sign of alpha atresia was the breakdown of the most advanced residual oocytes. Vacuoles (of various sizes) began to appear (Fig. 14A), merging to form large spaces within the decaying oocyte. The overall diameter of oocytes decreased from 600 to 300–400 µm; however oocytes retained their overall shape during alpha atresia and showed no signs of collapse (Fig. 14B). Beta atresia was the shortest phase. The oocytes had shrunk in size (<300 µm) but retained their previous overall structure and shape. A distinct hollow matrix retaining only the outer layers of the oocyte (follicle layers and the vitelline membrane) was the defining characteristic for beta atresia (Fig. 14C). The tissue retained this structure while the oocyte continued to decrease (150–180 µm). During gamma atresia the oocytes collapsed (Fig. 14D) or shrank. Some vacuoles remained in partially collapsed oocytes, but they were fewer in number and smaller in size (<150 µm) (Fig. 14E). The areas in and around the collapsed oocytes and ovarian lumen became more vascularized during this stage, and this helped facilitate rapid resorption of decaying cellular material (Fig. 14F). Undeveloped oocytes became more visible and numerous. Gamma atresia ended when only masses of broken-down cellular material remained. Delta atresia was characterized by the presence and decay of nondescript cellular material from the previous spawning (Fig. 14G). Delta atresia was present in approximately 30% or more of the ovary. There was also a decrease in the amount of vascularization within the ovarian lamellae during this stage because most of the old oocyte material had been resorbed. The lamellae contained only undeveloped oocytes and all the remaining material from the previous spawn was concentrated medially in the lamellae.

In the resting stage, no reproductive activity occurred in the ovaries. Infrequently, resting ovaries showed some minor evidence of the previous spawning. The remaining undeveloped oocytes were previtellogenic and varied widely in size (80–120 µm). The ovary wall was relatively thick, particularly in comparison to the

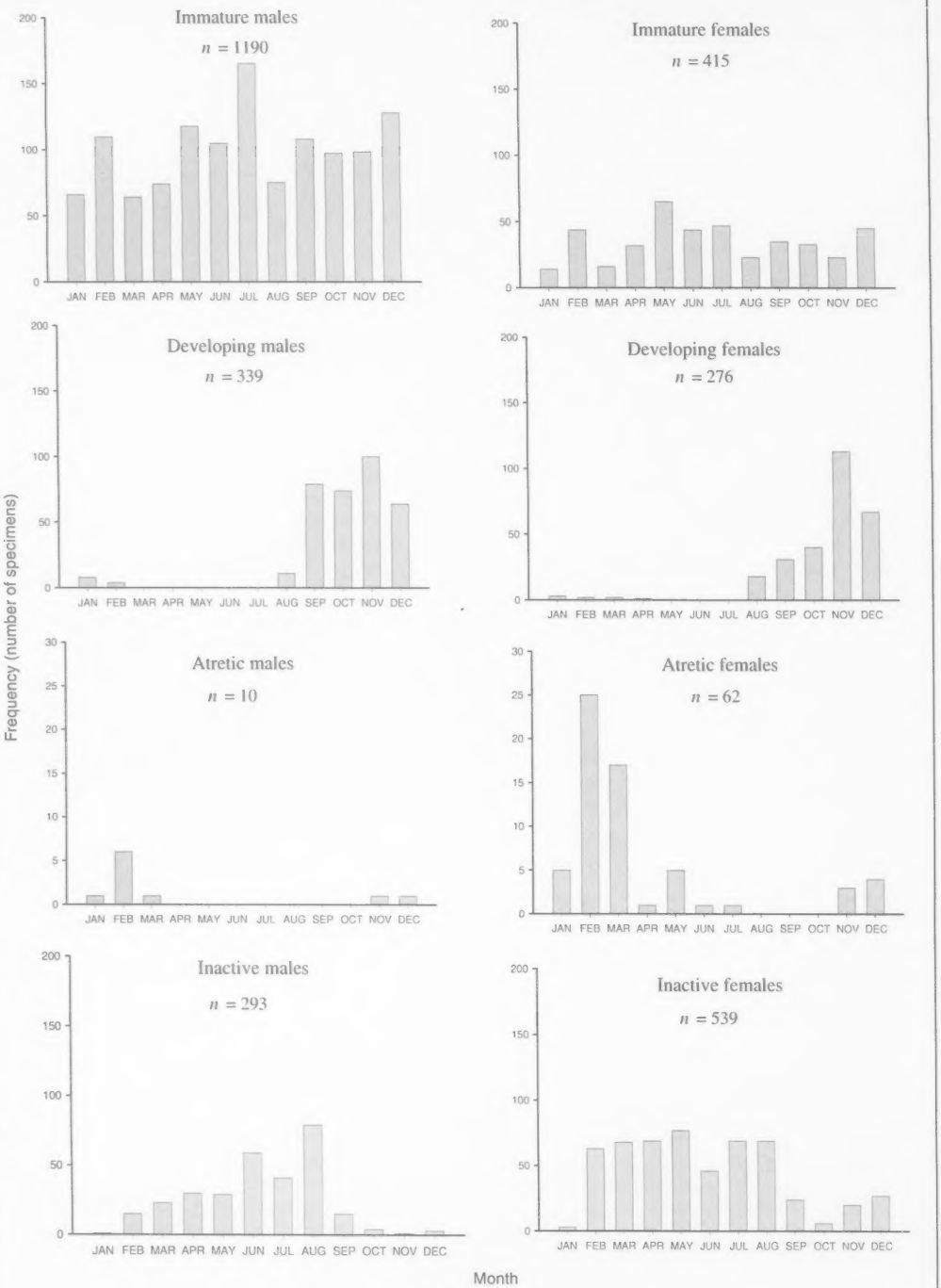


Figure 9

Frequency of occurrence of each maturity stage by month for male and female striped mullet (*Mugil cephalus* L.) from South Carolina estuaries, October 1997 to December 2000.

immature ovaries, and had distinct smooth muscle layers (Fig. 14H). Any stromal tissue left in the ovary at this point was also greatly reduced and was essentially the mesentary from which the lamellae were suspended.

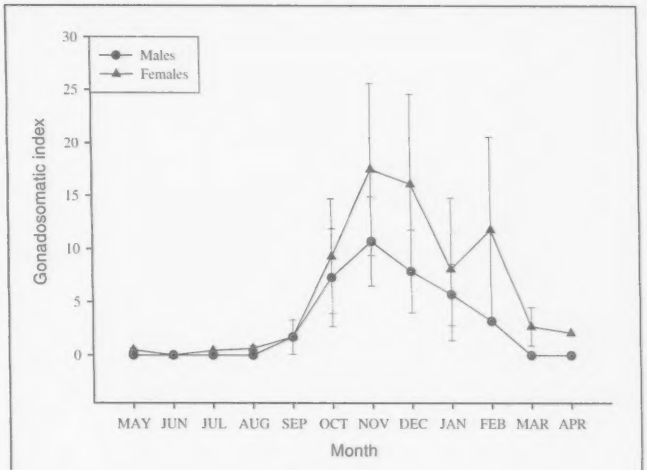


Figure 10

Mean gonosomatic index value by month for male and female striped mullet (*Mugil cephalus* L.) from South Carolina estuaries from 1998 to 2000. n=455.

Discussion

Age structure

The abundance of 1- and 2-year-old striped mullet in South Carolina indicated that immature fish dominate the estuarine population. The importance of proper age validation in order to make comparisons of age and sexual maturity cannot be understated. The most important aspect of age validation is to obtain a degree of precision that allows repeatability in age determinations (Campana, 2001). The periodicity of growth increment formation was validated by marginal increment analysis, and the precision of these age estimates was then tested by comparing age counts of two independent readers.

Marginal increment analysis showed that annual growth increments were deposited in striped mullet in July in the entire data set, as well as separately for ages 1–5. By validating increment periodicity separately for different age groups, a consistent pattern for the species can be determined (Campana et al., 1995; Campana, 2001). The percent agreement between the two readers and a t-test for independent age determinations allowed direct comparisons of the two groups of ages for consistency (Campana et al. 1995). However, these two methods were both independent of the age of the species. Therefore, average percent error (APE) was used to compare the different sets of ages because it is not independent of the age of a species (Beamish and Fournier, 1981). The low APE (0.41%) found between the two different age estimates indicated a high degree of precision, which allowed acceptance of these age determinations.

Sexual differentiation

Striped mullet are gonochoristic and sex is genetically determined. In contrast to mammals, gender of the mature germ cells of teleosts present in the gonad rather than the gender of the duct system forms the basis for classifying an individual as male or female (Shapiro, 1992). Early duct structures of the undifferentiated gonad characteristic of male development regress on female development. Initial duct development, along with germ tissue placement, takes on characteristics of the eventual sex once the process of differentiation begins (Asoh and Shapiro, 1997). Because of the plasticity of their gonad development, striped mullet retain some characteristics of the opposite sex (such as singular oogonia in males or duct-work in females) during the initial stages of differentiation. The term that has been used to describe this phenomenon is "intersex" (Yamamoto, 1969) but this state could more accurately be defined as the hermaphroditic stage of some gonochoristic species. Numerous descriptions of intersex exist for teleosts (Atz,1964). Previous studies have brought up the possibility of hermaphrodism in striped mullet (Stenger, 1959; Atz, 1964; Moe, 1966); however, there is only one example of a simultaneous hermaphroditic striped mullet in the literature (Franks et al., 1998). Once differentiation advances, these secondary characteristics atrophy, and the gonad develops toward the genetically determined sex.

We found that at first annular increment deposition (15–19 months), most (95%) immature striped mullet were sexually differentiated. Chang et al. (1995), using cultured striped mullet, found that differentiation began only after 12 months of age, and 70% to 90% of immature fish at 15 to 17 months had differentiated sexually. We found only a small percentage (1.2%) of differentiated specimens at 12 months of age. Chang et al.(1995) did not report fish sizes, and Stenger (1959) studied sizes at sexual differentiation without reporting age. Stenger (1959) concluded that striped mullet up to 150 mm generally were not differentiated sexually. We found four specimens in which differentiation had occurred in the 126–150 mm size range, which represented specimens 12 months or less in age. Once our specimens reached the 176–200 mm size range, just over 60% had sexually differentiated, which was also approximately the size range at which the first annulus appeared (Wenner and McDonough[3]).

Chang et al. (1995) found that females differentiated earlier than males; we, on the other hand, showed sex

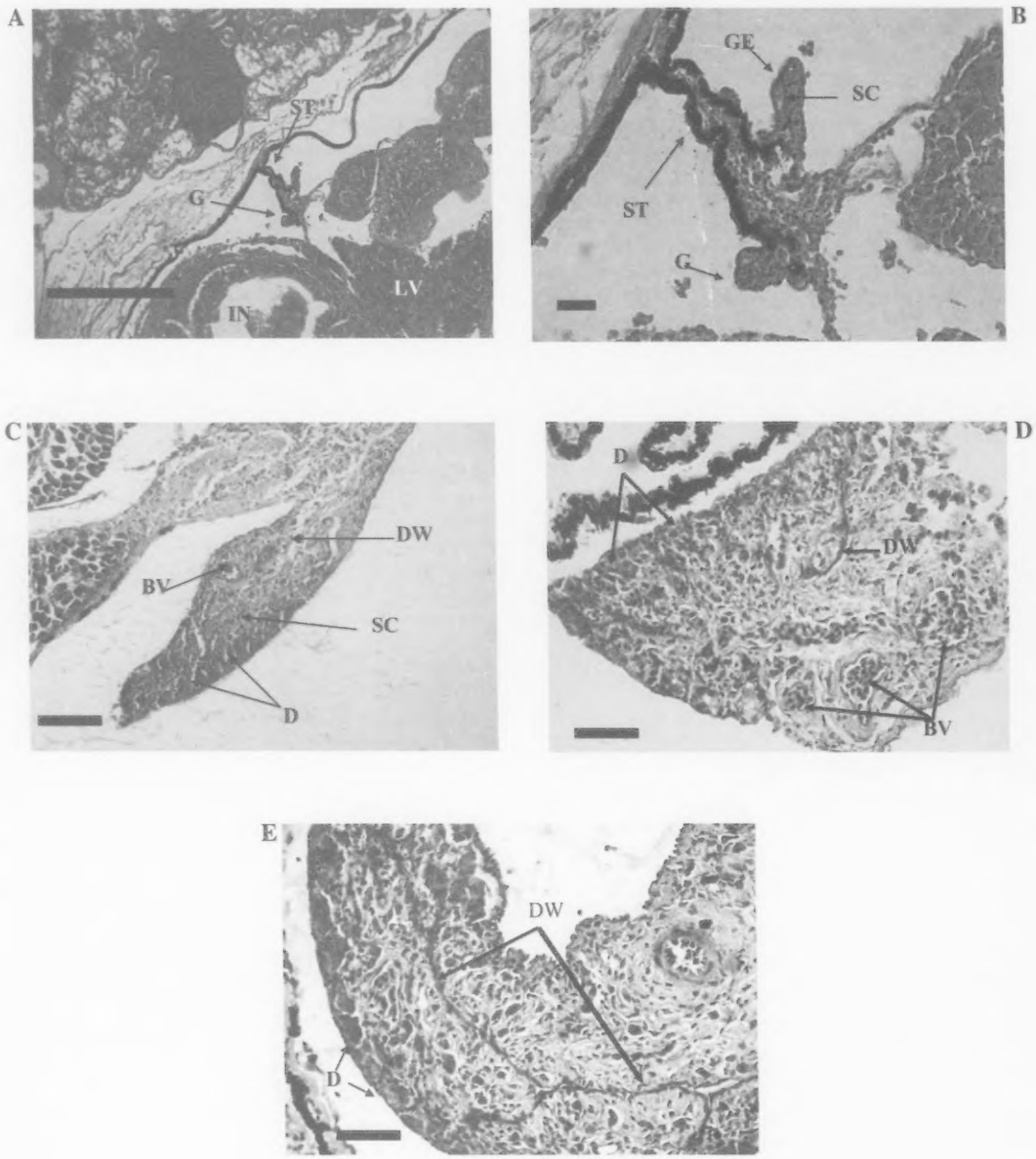


Figure 11

Photomicrographs of histological sections of undifferentiated juvenile striped mullet (*Mugil cephalus* L.) (**A**) 35-mm specimen at 100× (scale bar=50 μm) and (**B**) 600× (scale bar=10 μm) respectively; (**C**) 55-mm specimen at 400×, scale bar=20 μm; (**D**) 135-mm specimen at 400×, scale bar=20 μm; (**E**) 184-mm specimen at 400×, scale bar=20 μm (see text for detailed descriptions of each). Labels: G = primordial gonad; GE = germinal epithelium; SC = somatic cells; D = deuterogonia, DW = duct work; BV = blood vessel; ST = suspensory tissue; LV = liver; IN = intestine.

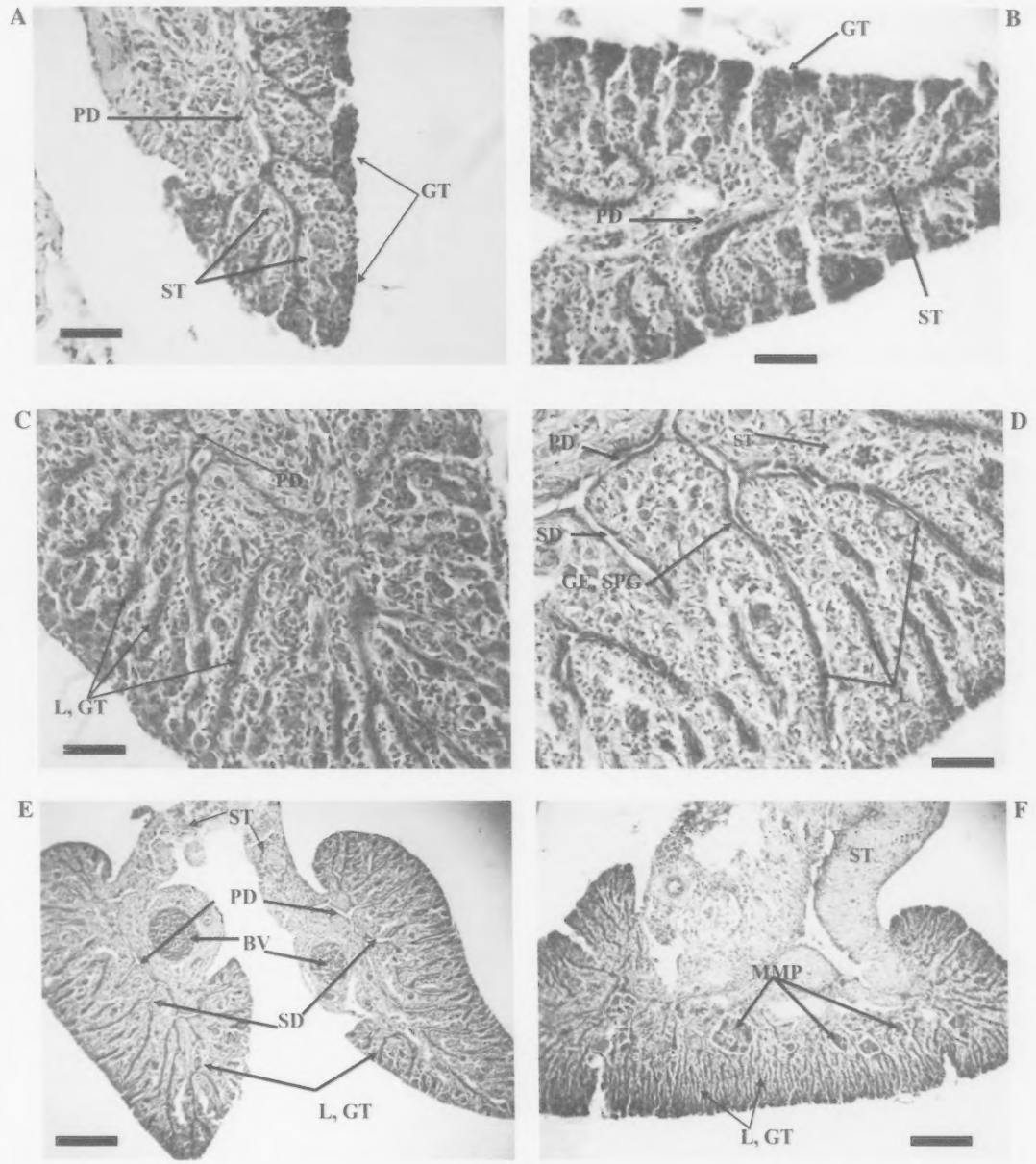
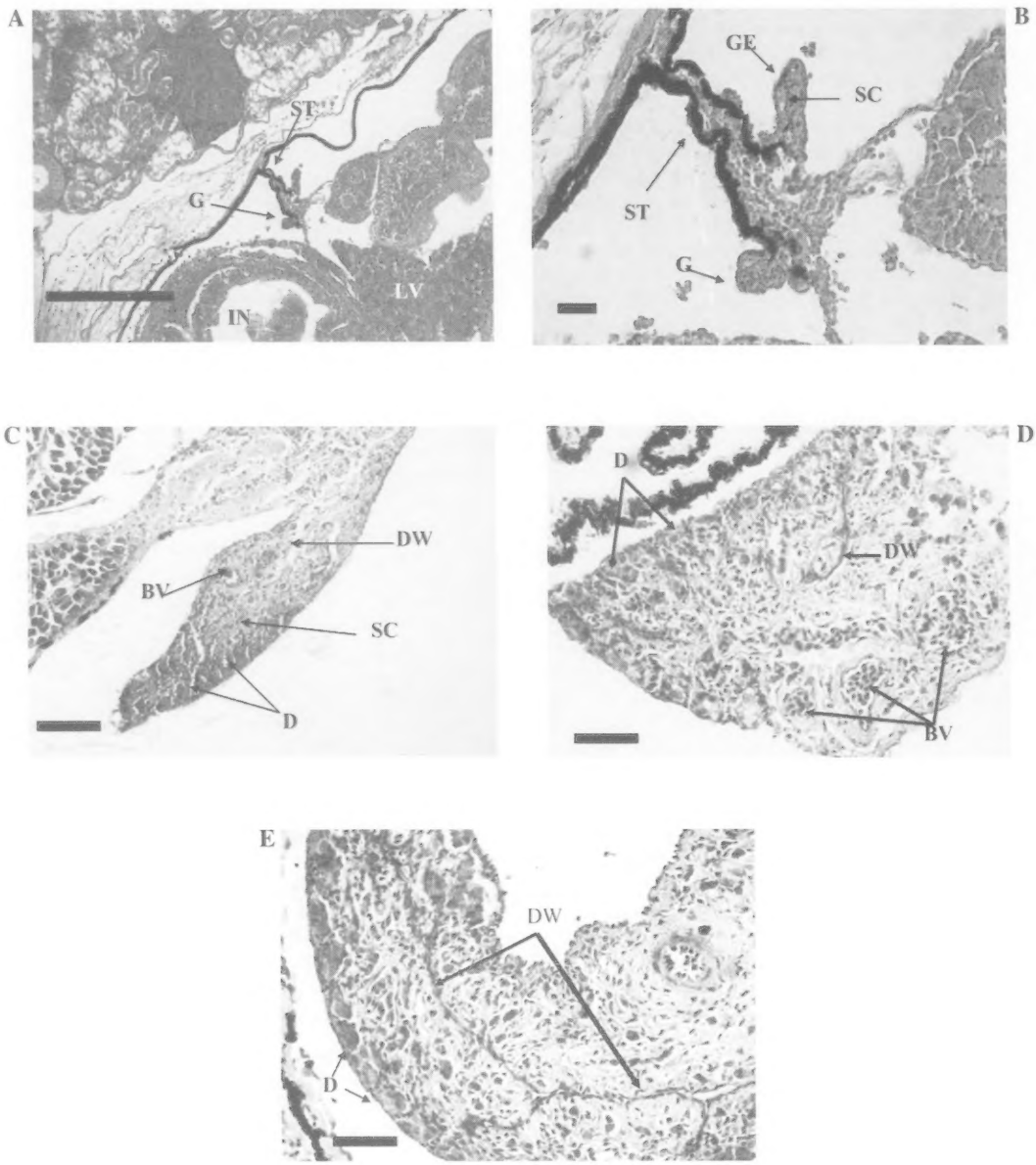


Figure 12

Photomicrographs of histological sections of sexually differentiating male striped mullet(*Mugil cephalus* L.) . (**A**) Early differentiation of a 164-mm specimen at 400×, scale bar=20 μm; (**B**) early differentiation of a 204-mm specimen at 400×, scale bar=20 μm; (**C**) advanced sexual differentiation of a 247-mm specimen at 100×, scale bar=100 μm; (**D**) advance sexual differentiation of a 258-mm specimen at 400×, scale bar=20 μm; (**E**) same specimen as previous photo at 100× showing full differentiation, scale bar=250 μm; (**F**) differentiated testes with melanomacrophages centers present in a 261-mm specimen, scale bar=250 μm (see text for detailed descriptions). Labels: ST = somatic tissue; GT = germ tissue; PD = primary duct; SD = secondary ductwork; BV = red blood vessels; GE = germinal epithelium; SPG = spermatogonia; MMP = melanomacrophages; L = lobule.



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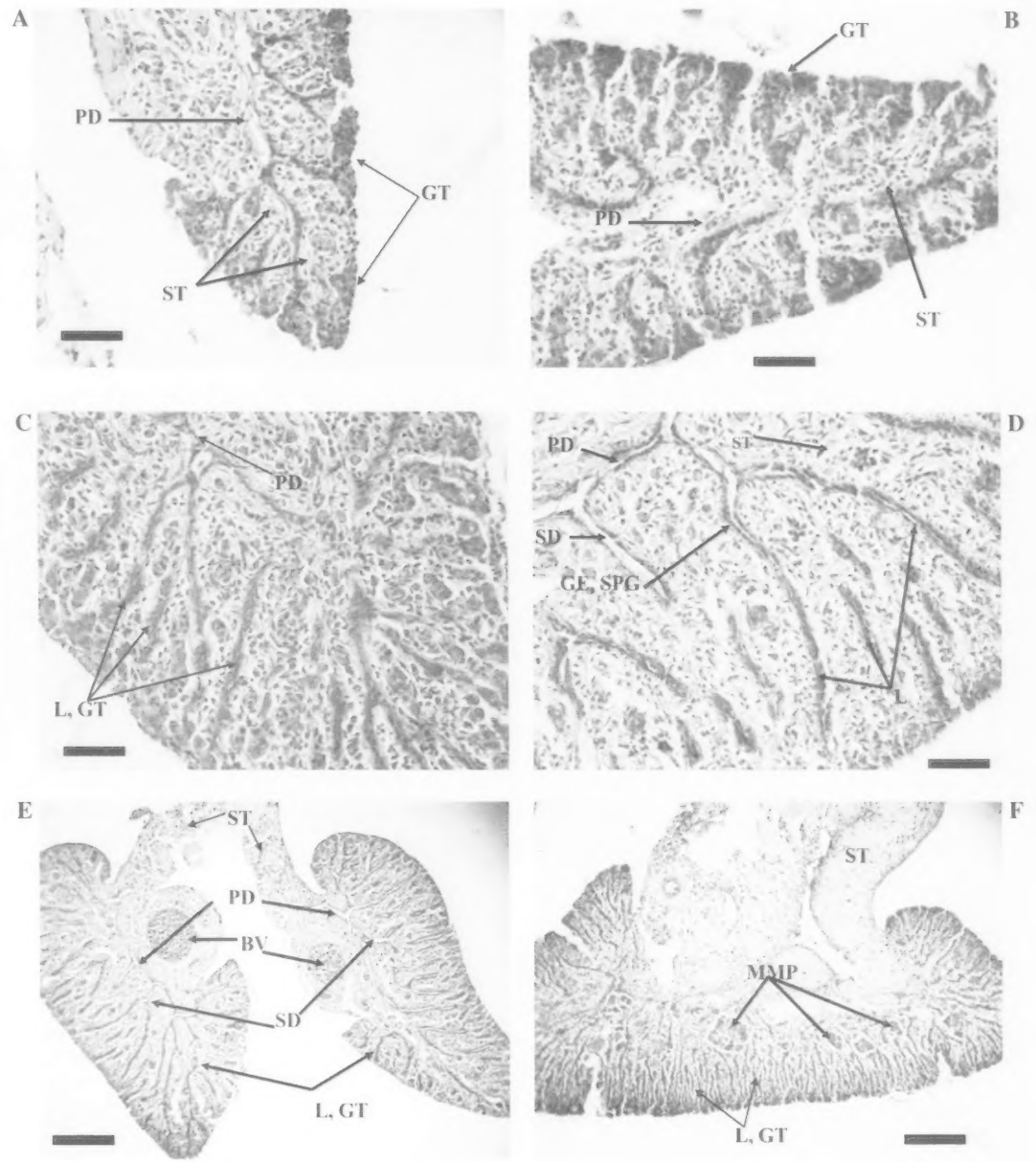

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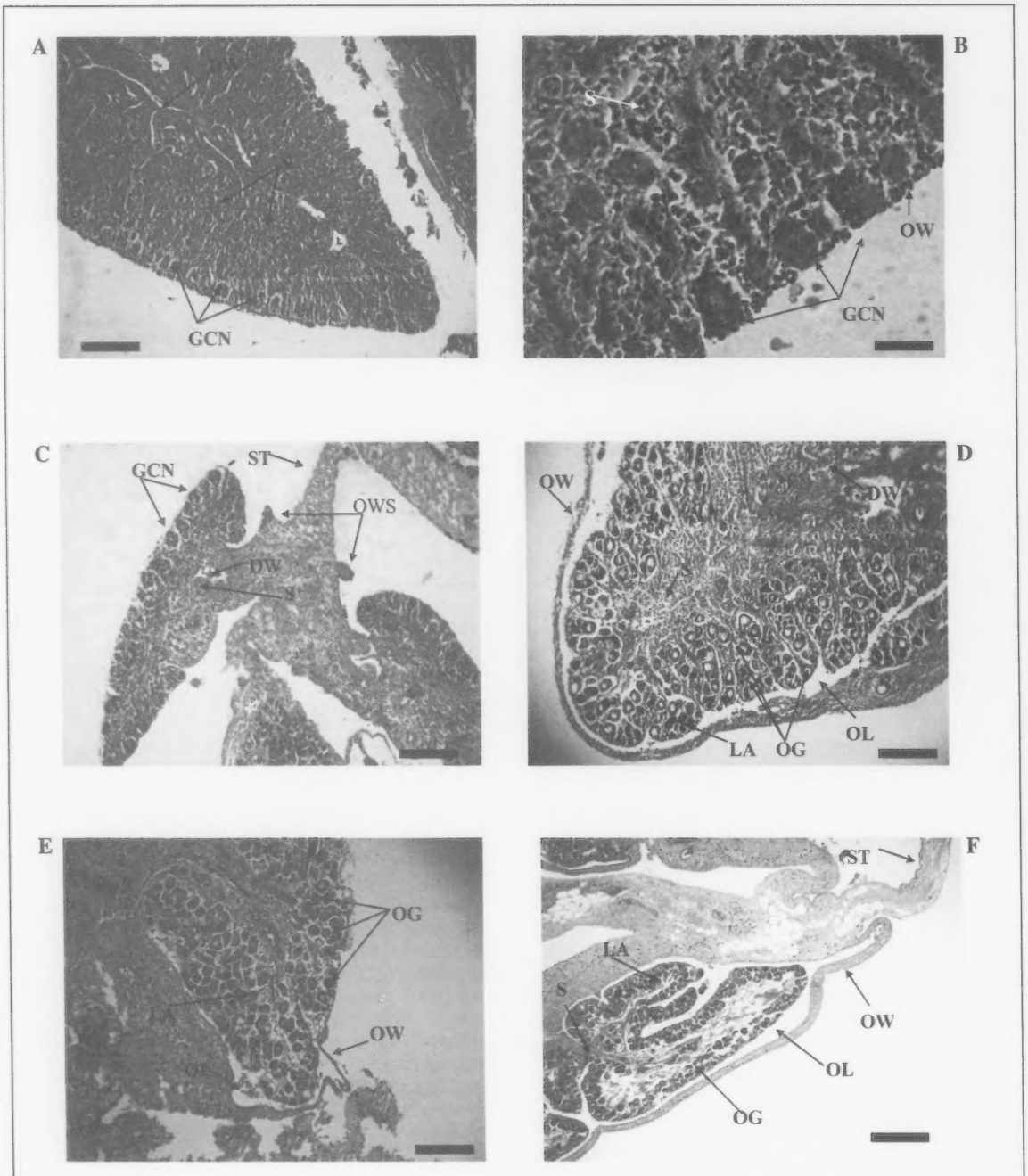

Figure 13

Photomicrographs of histological sections of sexually differentiating female striped mullet (*Mugil cephalus L.*). (**A**) Early differentiation of germ cell nests in a 239-mm specimen at 100×, scale bar=100 μm; (**B**) early differentiation of germ cell nests in a 205-mm female at 400×, scale bar=20 μm; (**C**) mid-differentiation in a 225-mm female at 100×, scale bar=100 μm; (**D**) advanced sexual differentiation with developing lamellae and ovarian wall in a 279-mm female at 100×, scale bars=100 μm; (**E**) advanced sexual differentiation in a 267-mm female at 100×, scale bar=100 μm; (**F**) full differentiation of a 284-mm female, scale bar = 100 μm. Labels: GCN = germ cell nests; OW = ovary wall; ST = suspensory tissue; OWS = ovary wall stalks; S = stroma; OG = oogonia; LA = lamellae; DW = ducts; OL = ovarian lumen.

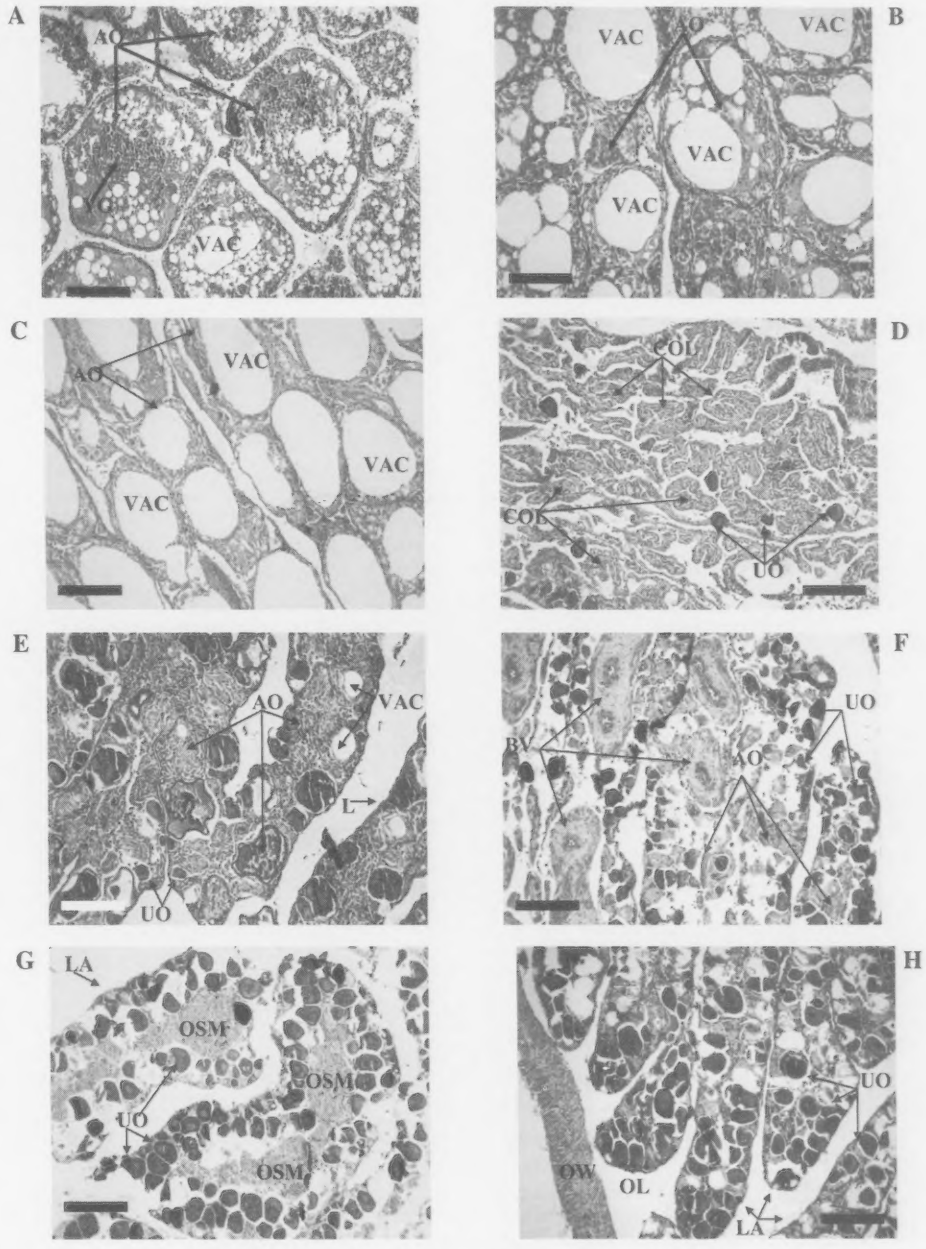

Figure 14

Photomicrographs of histological sections of ovarian atresia and the inactive reproductive stage in mature female striped mullet (*Mugil cephalus* L.). (**A**) Alpha-stage oocyte atresia, scale bar=100 μm; (**B**) Late alpha-stage oocyte atresia, scale bar=100 μm; (**C**) Beta-stage oocyte atresia, scale bar=100 μm; (**D**) Early gamma-stage oocyte atresia, scale bar=100 μm; (**E**) Gamma-stage oocyte atresia, scale bar=100 μm; (**F**) Late gamma-stage and early delta-stage oocyte atresia, scale bar=100 μm; (**G**) Delta-stage oocyte atresia, scale bar=100 μm; (H) Reproductively inactive striped mullet ovary with degraded cellular material from previous spawning, scale bar=100 μm. Labels: YG = yolk globules; VAC = vacuoles; AO = atretic oocytes; COL = collapsed outer cell layers; UO = undeveloped oocytes; BV = blood vessels; OSM = old spawn material; OW = ovary wall; OL =ovarian lumen; LA = lamellae.

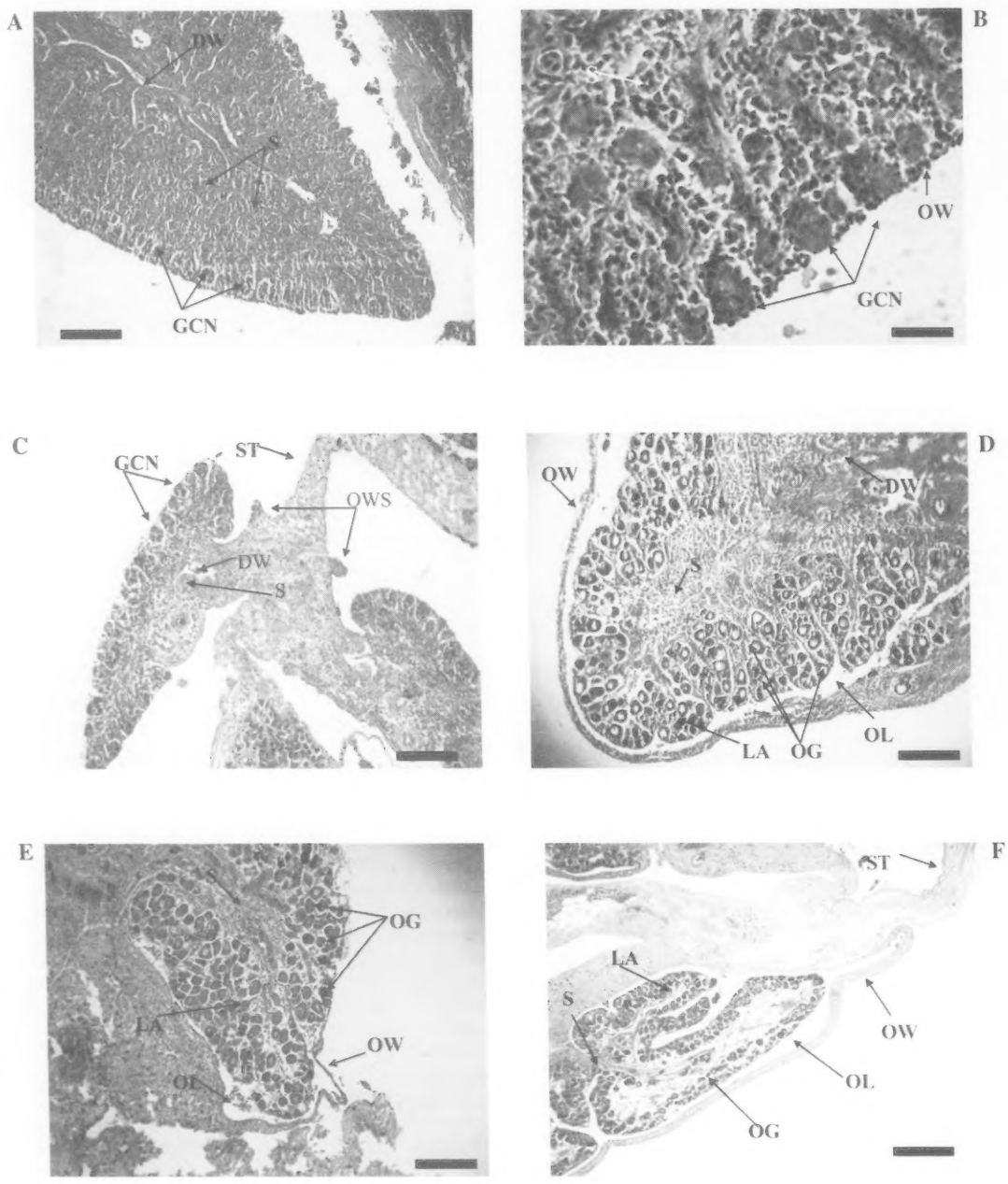

Figure 13

Photomicrographs of histological sections of sexually differentiating female striped mullet (*Mugil cephalus L.*). (**A**) Early differentiation of germ cell nests in a 239-mm specimen at 100×, scale bar=100 μm; (**B**) early differentiation of germ cell nests in a 205-mm female at 400×, scale bar=20 μm; (**C**) mid-differentiation in a 225-mm female at 100×, scale bar=100 μm; (**D**) advanced sexual differentiation with developing lamellae and ovarian wall in a 279-mm female at 100×, scale bars=100 μm; (**E**) advanced sexual differentiation in a 267-mm female at 100×, scale bar=100 μm; (**F**) full differentiation of a 284-mm female, scale bar = 100 μm. Labels: GCN = germ cell nests; OW = ovary wall; ST = suspensory tissue; OWS = ovary wall stalks; S = stroma; OG = oogonia; LA = lamellae; DW = ducts; OL = ovarian lumen.

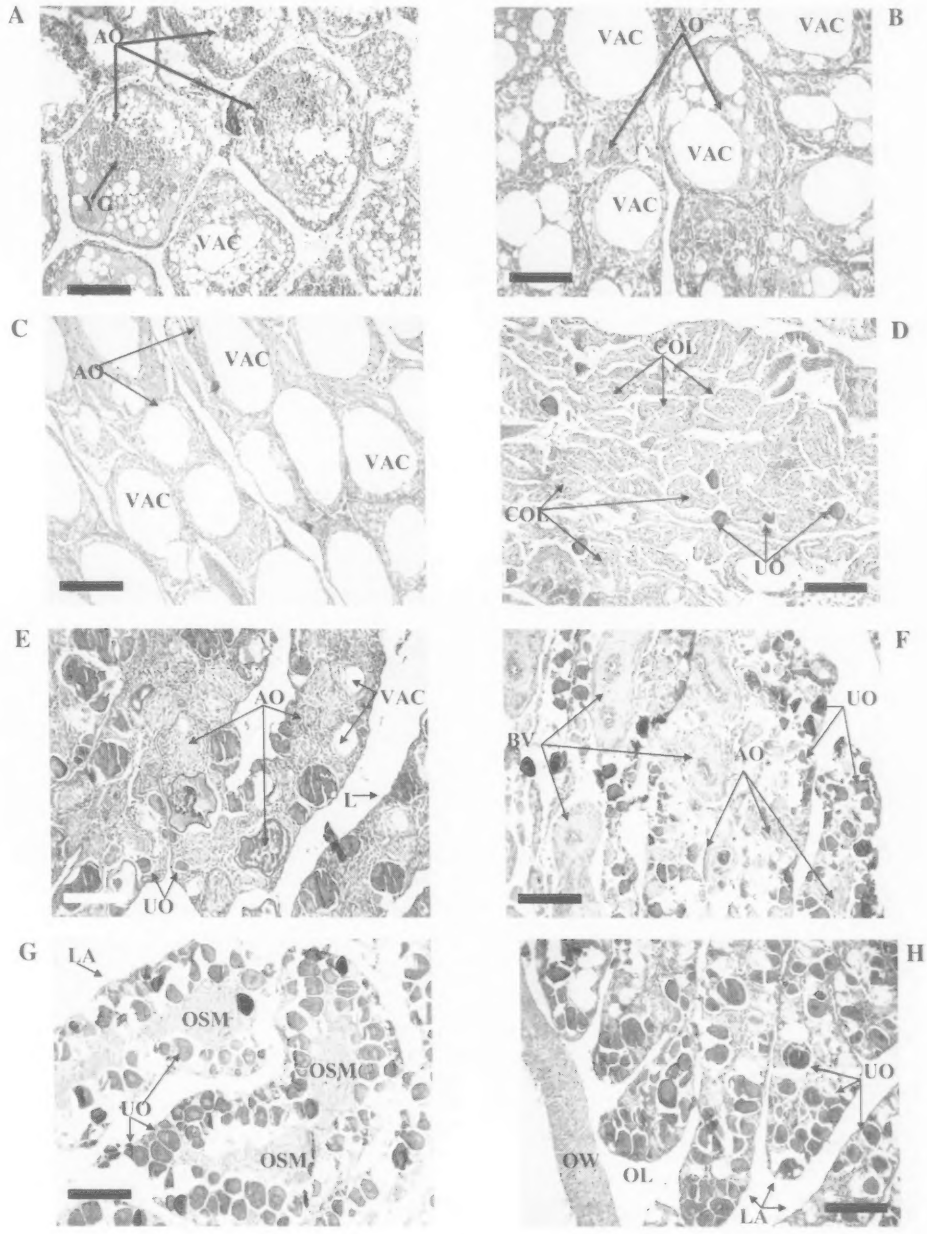

Figure 14

Photomicrographs of histological sections of ovarian atresia and the inactive reproductive stage in mature female striped mullet (*Mugil cephalus* L.). (**A**) Alpha-stage oocyte atresia, scale bar=100 μm; (**B**) Late alpha-stage oocyte atresia, scale bar=100 μm; (**C**) Beta-stage oocyte atresia, scale bar=100 μm; (**D**) Early gamma-stage oocyte atresia, scale bar=100 μm; (**E**) Gamma-stage oocyte atresia, scale bar=100 μm; (**F**) Late gamma-stage and early delta-stage oocyte atresia, scale bar=100 μm; (**G**) Delta-stage oocyte atresia, scale bar=100 μm; (**H**) Reproductively inactive striped mullet ovary with degraded cellular material from previous spawning, scale bar=100 μm. Labels: YG = yolk globules; VAC = vacuoles; AO = atretic oocytes; COL = collapsed outer cell layers; UO = undeveloped oocytes; BV = blood vessels; OSM = old spawn material; OW = ovary wall; OL =ovarian lumen; LA = lamellae.

ratios at size indicating that males differentiated first. This difference may be explained by the experimental methods because the differentiation process was likely similar between the cultured and wild fish. Chang et al. (1995) showed that female development occurred before male development based on levels of plasma sex steroids. However, this finding was later corrected to show that plasma sex steroid levels were the same for males and females throughout sexual differentiation (Chang et al., 1999).

The formation of lobules with the proliferation of germ tissue has been previously described as a male developmental pattern (Stenger, 1959; Grier, 1981; Grier and Taylor, 1998; Grier, 2000). The morphological progression seen in the present study was similar to that previously described in histological examinations of differentiation in striped mullet in conjunction with size (Stenger, 1959) and age (Chang et al., 1995). However, ours is the first study to examine sexual differentiation of both male and female striped mullet with changes in size and age and to describe these changes histologically.

The undifferentiated gonad appeared to have male morphological characteristics. The first morphological signs of female differentiation were the movement of deuterogonial germ-cell nests from the periphery of the gonad. This pattern of development was similar to the ontogeny of differentiation described previously for striped mullet (Stenger, 1959). However, the presence of the tissue stalk at the base of the suspensory tissue, to which the ovary wall was attached, has not previously been described. The tissue stalk was present on the majority (68%) of differentiating ovaries and only a few (0.25%) of the differentiating testes. The presence of this stalk in differentiating testes indicated that this characteristic alone should not be used to determine genetic sex. However, the presence of the tissue stalk, in addition to the rounded oogonial nests throughout the gonad, strongly indicated that the specimen was female. There were no specimens observed to be developing an ovary wall that also had developing lobules or duct-work (male characters). Therefore, from a morphological standpoint, the initial definitive identification of the differentiating ovary was the formation of the ovary wall along with rounded germ cell nests throughout the lobe. A primary duct at the center of the developing ovary was present at this stage but any secondary duct-work had begun to atrophy. It was also observed that oogonial and oocyte proliferation could occur throughout the lobe without a definitive ovary wall, which would also be a strong indicator of the female sex.

Size and age at maturity

Once sexual differentiation had occurred, the earliest indication of spermatogenesis occurred at just under 250 mm (two specimens) and one year of age. However, the majority of the developing specimens (89.9%) did not show signs of spermatogenesis until they reached 300 mm and age 2. The greater abundance of immature males under 300 mm would also indicate that full maturity was reached by this length. Almost all the males over 325 mm were in some state of reproductive activity, either developing or running, ripe, because most of these larger males were captured only during the spawning season. October, November, and December were the only months when we saw these larger fish, except for some atretic-stage specimens taken from freshwater during the spring. The first signs of spermatogenesis for striped mullet, both from eastern Florida (Stenger, 1959) and South Carolina, were found in August.

Greeley et al. (1987) did not age female striped mullet but used the growth schedule of Thomson (1966) to conclude that striped mullet in eastern Florida reach sexual maturity at 2.25 to 2.5 years, which is 1 to 2 years earlier than that previously reported (Jacot, 1920; Broadhead, 1956; Anderson, 1958; Thomson, 1966). One problem in earlier studies was the use of scale-based age estimates (Jacot, 1920; Thomson, 1951, 1966; Timoshek, 1973). The otoliths used in our study showed more repeatability than would scales. Age schedules based on scales were likely to contain problems with the error terms and overestimation. Another factor may have been the lack of a proper age-validaton protocol. The lag in time between the actual birthdate and the first increment formation was not incorporated into the age model. A fish with a single annular ring that appeared to be mature could actually have been up to 30 months old. Male striped mullet did not begin to mature until they were one year old, and almost 100% had reached sexual maturity by age 3. Ripe and atretic males were also found at age 1.

Size at maturity for female striped mullet was reported to be from 290 to 430 mm (Thomson, 1951, 1966; Broadhead, 1956; Chubb et al., 1981). This wide range in size at maturity depended on whether gonads were examined by gross morphological examination (Thomson, 1951, 1966; Broadhead, 1956) or histologically (Stenger, 1959; Chubb et al., 1981). Stenger (1959) found that oocyte development occurred in specimens as small as 270 mm fork length (300 mm TL). Greeley et al. (1987) reported the minimum size at maturity for female striped mullet in eastern Florida was 230 mm SL (290 mm TL). The minimum size at which a female was found to be undergoing active vitellogenesis in the present study was 291 mm. The first signs of female maturity were evident in small numbers (15) in the 2-year-olds. The first atretic females were also found at age 2. The age at maturity for female striped mullet in our study was similar to that found by Greeley et al. (1987) who used length-based predicted ages. Therefore, it appears that striped mullet in South Carolina have a similar maturity schedule to those found in eastern Florida.

Immature and inactive males and females were found every month of the year. The presence of ripe males from October through February and the presence of developing females from August through March support the idea of an extended spawning season from October through April.

The presence of developing females indicated reproductive activity through April: however numbers were small (McDonough et al., 2003). Most of the specimens collected in March and April were either immature or inactive. It has also been demonstrated that striped mullet in closed freshwater systems, such as impoundments, can begin reproductive development. However, unless artificially manipulated, spawning did not occur in freshwater and the fish resorbed the developed gametes (Shireman, 1975; Tamaru et al., 1994). The re-absorption of gametes would undoubtedly have a positive effect on growth rates and may contribute to some of the variation in size at age. Reproductively inactive (but mature) females present every month could indicate that mature mullet do not spawn every year or that fish that remain in the estuary do not migrate offshore to spawn. The most likely possibility would be that inactive females found in the early part of the spawning season may not spawn until much later. However, the presence of developing oocytes beginning in August would indicate that a few months were required for complete recrudescence. It has been shown that striped mullet undergoing the spawning migration between the Black Sea and the Sea of Azov required two months for full ovarian development (Apekin and Vilenskaya, 1978). Also, inactive females from the mid to late spawning season could have spawned early, returned to the estuary, and their ovaries could have regressed. We found no ripe female mullet in the estuaries during the entire study; their absence was likely due to their migration from coastal waters. Evidence of striped mullet spawning (through the back calculation of birthdates from daily growth increments from juveniles) has also shown that the spawning season extends from October through April (McDonough and Wenner, 2003).

Sexual development

It is not known what cue initiates gametogenesis in striped mullet, but it is generally accepted that changes in temperature and photoperiod help regulate the seasonal reproductive cycle (Anderson, 1958; Kuo et al., 1973; Greeley et al., 1987; Kelly et al., 1991; Render et al., 1995). It has been shown that although striped mullet can mature in a range of salinities, the best production is reached when their gonads develop in salinities of 13 to 35 ppt (Brusle, 1981; Tamaru et al., 1994). Previous studies of striped mullet (Kuo et al., 1974) and other fall spawning fishes that migrate offshore to spawn (de Vlaming, 1974; McQuarrie et al., 1978; Whitehead et al., 1978) have indicated that a shortening day length was the key stimulus for annual reproductive development and migration. Dindo and MacGregor (1981) demonstrated a high correlation between the levels of serum gonadal steroids and the gonadosomatic index in striped mullet during the reproductive cycle; a shortening photoperiod was suggested as the major factor in stimulating reproductive activity. In our study the most reproductively advanced specimens (late recrudescence) in freshwater were captured in October and no other specimens of similar development were captured during the rest of the spawning season in freshwater. In contrast, the majority of the specimens undergoing vitellogenesis were captured in the lower portions of the estuaries during November and December in salinities greater than 15 ppt. This finding indicated movement of these developing fish from the freshwater portions of the estuary toward the ocean for the spawning migration. This migration time-period also coincided with a mean monthly temperature decrease in temperature (from 21.8° to 13.6°C) and in photoperiod in both the freshwater and brackish portions of the estuaries.

The ovarian atretic process in female striped mullet was characterized by four distinct stages that followed a very similar progression to that described for the northern anchovy (Hunter and Macewicz, 1985). Our study is the first to describe the atretic process in striped mullet ovaries in detail and to apply the classification system developed by Hunter and Macewicz (1985). Knowledge of ovarian atresia is useful for the timing of spawning. However, the lack of immediate atretic-stage fish, with indicators such as postovulatory follicles, prevented us from determining the temporal duration of the different atretic stages. The detailed morphological descriptions of ovarian atresia presented in our study would be of value for future studies to determine the specific timing of the atretic process.

The histological descriptions for male and female developmental stages in association with both size and age data provide a clear picture of these parameters at differentiation and maturity in South Carolina striped mullet. Previous studies of striped mullet reproduction concentrated on just one sex or used cultured fish extensively and may have considered size or age but not both in a single study. Because of the length of the undifferentiated gonad stage in juvenile striped mullet, previous studies have proposed the possibility of protandric hermaphrodism in this species. However, the results of our study indicated that striped mullet are gonochoristic but capable of nonfunctional hermaphroditic characteristics in differentiated mature gonads. It is hoped that the descriptions of developmental morphological features presented in the present study will be useful for future studies by providing a key to reproductive ontogeny that relates directly to somatic growth and age in striped mullet. In particular, the morphological characteristics of sexual differentiation could enable more precise determinations of sex in immature mullet, which, in turn, would indicate the sex ratio of males and females in a given population and allow the development of better management strategies.

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Abstract—Large pelagic sharks are caught incidentally in the swordfish and tuna fisheries of the Mediterranean Sea. In our study, twelve shark species were documented as bycatch over three years from 1998 to 2000. Blue shark (*Prionace glauca*) was the predominant species in all gears and areas examined. Shortfin mako (*Isurus oxyrinchus*), common thresher shark (*Alopias vulpinus*), and tope shark (*Galeorhinus galeus*) were the next most abundant shark species—found in more than half of the areas sampled. Catch composition varied both in the areas and gears investigated. Sharks represented 34.3% in weight of total catches sampled in the Alboran Sea and 0.9% in the Straits of Sicily. Higher shark catches were observed in the swordfish longline fishery, where a nominal CPUE value reached 3.8 sharks/1000 hooks in the Alboran Sea. Size distribution by fishing gear varied significantly. Albacore longline catches consisted mainly of juveniles, whereas subadult and adult specimens were more frequent in the swordfish longline and driftnet fishery. The percentage of sharks brought onboard alive was exceptionally high; only 5.1% of the specimens died. Few discards (seven blue shark) were recorded in the Greek longline fleet during onboard sampling in the Aegean Sea.

Incidental catch and estimated discards of pelagic sharks from the swordfish and tuna fisheries in the Mediterranean Sea

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Fish. Bull. 103:620–634 (2005).

The effect of fishing on shark stocks has become the focus of considerable international concern. The fishery-induced depletion of stocks is made worse by the slow growth, late maturity, and low fecundity of sharks, all of which make them extremely vulnerable even to modest levels of fishing. Although no pelagic shark-directed fishery exists in the Mediterranean Sea, other pelagic fisheries may be a great threat, because species with higher production rates, such as swordfish and tuna, continue to support the fishery while species with lower rebound potential are driven to stock collapse or extirpation (Musick et al., 2000). In recent years sharks, which were once considered bycatch (and discarded), have become a target species of the Spanish swordfish fleet because highly restrictive measures regulating swordfish catch have been established in the Atlantic Ocean, coupled with the fact that the international market is now more open to pelagic sharks and their derivatives (Mejuto and de la Serna, 2000).

Most pelagic sharks are migratory species. Thus, effective management proposals require reliable data that reflect migratory patterns, and multilateral international agreements are needed between all Mediterranean countries involved. During the last 40-year period, Spanish, Italian, and Greek longline and driftnet fleets have operated throughout the Mediterranean, targeting mainly swordfish or albacore and bluefin tuna. Catches began to expand slowly after 1962, increased rapidly with the advent of monofilament driftnets, and peaked in the late 1980s (Anonymous, 1999). Until recent years sharks were the most abundant incidental catch (landed, but not specifically targeted, or discarded). But they may become

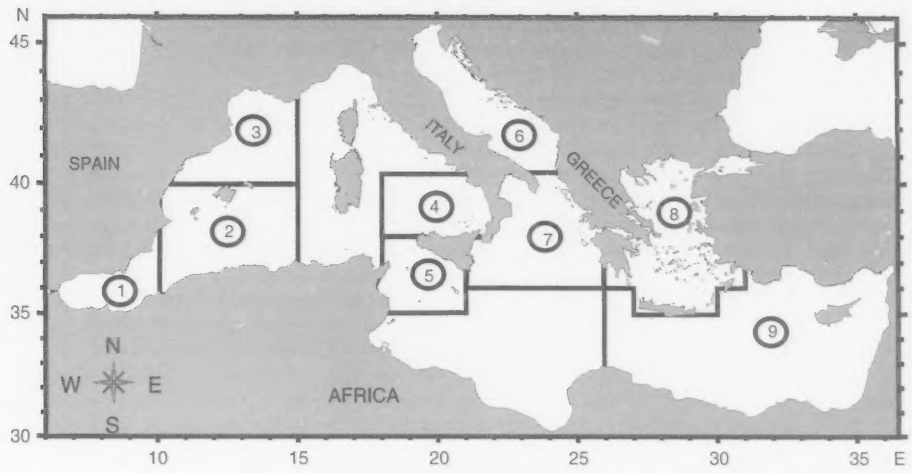

Figure 1

Map of the Mediterranean Sea, showing the nine study areas used for sampling sharks during 1998–2000. 1=Alboran Sea, 2=Balearic Islands area, 3=Catalonian Sea, 4=Tyrrhenian Sea, 5=Straits of Sicily, 6=Adriatic Sea, 7=Ionian Sea, 8=Aegean Sea, and 9=Levantine basin.

target species because their current low market value now appears to be increasing. Many of the data requirements of pelagic shark assessment are similar to those for assessing other highly migratory species: knowledge of stock structure, age and growth rates, natural mortality rates or fishery statistics. However, there is scant information about either the population biology or the catch levels of most incidental species. Primary literature on pelagic shark incidental catch in the Mediterranean Sea is rare and relates only to subareas that are not studied in a coordinated manner (De Metrio et al., 1984; Filanti et al., 1986; Buencuerpo et al., 1998; Di Natale, 1998; Mejuto et. al., 2002). ICCAT reports on pelagic shark catch show great annual variation in catch statistics and are fragmented because not all countries submit data for the entire time series. Catches of Selachii reported by FAO statistics for Spain, Italy, and Greece in the Mediterranean amount to 4209 metric tons in 2000, but include pelagic and benthic sharks, skates, rays, and chimaeras together.

Given the scarcity and heterogeneity of the available data, an international project was established (Megalofonou et al.[1]) to collect fishing and biological data with standardized methods from all commercial fisheries of the European countries that catch pelagic sharks in the Mediterranean. This article presents the results of the investigations carried out by observers at landing sites and onboard fishing vessels that target swordfish and tunas with longlines and driftnets. The main objective of this study was to analyze shark incidental catch and discards and to provide information on species composition, distribution, and abundance. The status of each shark brought on board (alive, dead, or damaged) and the disposition of sharks caught on some vessels (kept or discarded) were examined by using onboard observations to obtain essential data for effective fisheries management.

Materials and methods

Sampling areas

The Mediterranean Sea is a semi-enclosed area with pronounced oligotrophy in the surface waters due to small amounts of nutrient discharge from the land. The shallow and narrow Strait of Gibraltar connects it to the Atlantic. It consists of two nearly equal-sized basins, the eastern and the western basin, connected through the narrow and shallow Straits of Sicily. A network of sampling ports throughout the Mediterranean was established in order to cover a wide range of fishing grounds, fleets, and gears. The sampling areas, shown in Figure 1, were the following: the Alboran Sea (1), the Balearic Islands area (2), the Catalonian Sea (3), the Tyrrhenian Sea (4), the Straits of Sicily (5), the Adriatic Sea (6), the Ionian Sea (7), the Aegean Sea (8), and the Levantine basin (9). Researchers from Greece, Italy, and Spain were involved in data collection concerning incidental catch of pelagic sharks in the Mediterranean Sea.

[1] Megalofonou, P., D. Damalas, C. Yannopoulos, G. De Metrio, M. Deflorio, J. M. de la Serna, and D. Macias. 2000. Bycatches and discards of sharks in the large pelagic fisheries in the Mediterranean Sea. European Union Project 97/50 Directorate General XIV/C1, 336 p. Directorate-General for Fisheries and Maritime Affairs, European Commission, Rue Joseph II, 99, B-1049 Brussels.

Description of gear

Fleets sampled by observers targeted swordfish (*Xiphias gladius*), albacore (*Thunnus alalunga*), or bluefin tuna (*Thunnus thynnus*). Five fishing gears were studied: swordfish longline (SWO-LL), "American type" swordfish longline ($SWO\text{-}LL_A$), albacore longline (ALB-LL), bluefin tuna longline (BFT-LL), and driftnet (DN).

The swordfish longline consists of a nylon monofilament main line, 2 to 3 mm in diameter, hung in a sagging curve between surface floats. Branch lines with a length of 5–18 m descend from the main line, each terminating in a single baited J-hook. The number of hooks ranges from 800 to 2800 and hook size varies from no. 0 to 5. The "American type" swordfish longline, a variation of the aforementioned gear and used mainly in Greece, was introduced in the Greek fishery in the mid 1980s. It consists of fewer hooks (350–700) of size 2, much longer branch lines (15–50 m), and a fish attractant light stick (Duralumes® Lindgren-Pitman Inc., Pompano Beach, FL) attached to each branch line, 1 m above the bait. The albacore longline is a more lightly constructed longline that has 800 to 4000 J-hooks, hook sizes 6–9, a main line from 1 mm to 1.6 mm in diameter, and shorter branch lines (3–6 m). The bluefin tuna longline is the most robust longline, having 1000 to 1200 J-hooks of size 0 or 1, a main line 5.0 mm in diameter, and branch lines 45 m long. Frozen mackerels (*Scomber scombrus*) or (*Scomber japonicus*) and frozen squids (*Illex* sp.) or (*Loligo* sp.) are used as baits, as in the swordfish and bluefin tuna fishery, whereas frozen sardines—*Sardina pilchardus* or *Sardinella* sp.—are the baits mainly used in the albacore fishery. Driftnets, ranging from 2.5–20 km in length and from 24–40 m in height and having a stretched mesh size of 380 mm, were used mainly in Italy by the swordfish and tuna fishery. Since 1998, after the enforcement of the regulatory measures for the driftnets, the traditional nets were rejected and the Italian fishermen introduced a smaller driftnet, called ferrettara. This net has a length of 2.5 km, a depth from 18 to 25 m, and a mesh size of 180 mm. All gears targeting large pelagic fish, both longlines and nets, are shot (deployed) in the evening and their retrieval begins after midnight. Among the gears sampled, the swordfish longline is the main gear used in the Mediterranean Sea.

Data collection and statistical analyses

Sampling was carried out during a three-year period from 1998 to 2000. Catch and effort data were derived from records taken by observers stationed both at main fishing ports and onboard 11 commercial fishing vessels, from January 1998 to December 1999. Biological data, such as size and sex of sharks caught, were obtained from January 1998 to September 2000. Observers were present on fishing trips (702 fishing days) and at 17 landing sites, performing duties that included collecting fishing and operational data, identifying and measuring fish, as well as recording the exact location and date for each fishing set. From each fishing vessel sampled at-sea, these observers collected the following fishing and operational data series: name of fishing boat, gear used, duration of each trip in days, fishing effort per fishing day (number of hooks for longline gear, net length, and depth in meters for driftnet gear), number and weight of fish caught per fishing day by species, and number of sharks discarded. Because fishermen generally do not keep reliable logbooks to report their daily catch, sampling at landing sites was performed through interviews, as well as by direct observations and measurements. From each boat sampled at the landing site, observers, interviewing fishermen or skippers of the vessels, collected data on the duration of each trip in days, the number of fishing days, the fishing area, and the fishing effort per fishing day. The number and weight of fish landed were observed and measured directly during landing and recorded by species. Biological data for the specimens caught included total length (TL) in cm, fork length (FL) in cm, dressed weight (to the nearest 0.1 kg), and sex when possible.

To investigate trends in the abundance of sharks, we used the nominal catch per unit of effort (CPUE) expressed as the number of individuals per 1000 hooks for longlines, and per 1000 m of net for driftnets. Fishing duration was assumed to be constant because soak time was almost the same for all trips. Setting began at dusk and retrieving began after midnight. Each shark brought onboard vessels was assessed according to the following scale: 1) good—very high motility and active behavior; 2) fair—moderate motility; 3) poor—poor motility but having the ability to respond to external stimuli; 4) dead or showing no response to external stimuli.

Chi-square (χ^2) tests were performed to test variations in species composition by type of fishing gear, area sampled, and by sampling onboard or at landing sites. Catch data were classified in rows (species) and columns (gears, areas sampled, or sampling venue [fishing vessel or landing site]) to create contingency tables and were tested for significant association between rows and columns, assuming that row and column classifications are independent (null hypothesis). Nonparametric analysis of variance (Kruskall-Wallis test) was performed to compare the total length medians of the samples by fishing gear and per area. Nonparametric analysis of variance was used because our data sets did not meet the criteria needed to use the classical method of analysis of variance (ANOVA) e.g., normally distributed populations, equal variances.

Results

A total of 8733 sharks (153.6 t biomass) and 131,912 fish of other species (teleosts, rays, and skates) were documented from 5826 fishing days sampled, 5124 at landing sites and 702 onboard, during the two-year period 1998–99 (Tables 1–2). In all areas examined throughout the Mediterranean Sea, sharks represented

Table 1

Fishing sets by gear type and number of sharks caught (landed, plus discarded) throughout the Mediterranean areas studied during 1998–99 on selected vessels observed at-sea and recorded at landing sites. Area numbers: 1=Alboran Sea, 2=Balearic Islands area, 3=Catalonian Sea, 4=Tyrrhenian Sea, 5=Straits of Sicily, 6=Adriatic Sea, 7=Ionian Sea, 8=Aegean Sea, and 9=Levantine basin). Gear abbreviations: SWO-LL=swordfish longline, ABL-LL=albacore longline, BFT-LL=bluefin tuna longline, DN=driftnet, SO-LL_A=American-type swordfish longline. PG=*Prionace glauca*, IO=*Isurus oxyrinchus*, AV=*Alopias vulpinus*, GG=*Galeorhinus galeus*, LN=*Lamna nasus*, AS=*Alopias superciliosus*, SZ=*Sphyrna zygaena*, HG=*Hexanchus griseus*, CP=*Carcharinus plumbeus*, SB=*Squalus blainvillei*, MM=*Mustelus mustelus*, CM=*Cetorhinus maximus*.

	Number of fishing sets					Number of sharks caught										
Area	SWO-LL	ALB-LL	BFT-LL	DN	SWO-LL_A	PG	IO	AV	GG	LN	AS	SZ	HG	CP	SB	CM	MM
1	1391	0	0	0	0	5057	268	11	10	0	6	1	0	0	0	0	0
2	1312	48	19	0	0	85	42	17	4	0	0	0	0	0	0	0	1
3	290	41	0	0	0	97	3	2	2	0	0	0	0	0	2	0	0
4	9	0	0	0	0	5	0	0	0	0	0	0	0	0	0	1	0
5	23	7	2	0	0	3	0	1	1	0	0	0	3	2	0	1	0
6	771	6	0	0	0	2053	0	8	0	1	0	2	0	0	0	0	0
7	594	239	0	715	0	938	0	21	0	14	0	1	0	0	0	0	0
8	0	99	0	0	42	28	0	1	1	0	0	0	0	0	0	0	0
9	7	0	0	0	211	29	8	1	1	0	1	0	0	0	0	0	0
Total	4397	440	21	715	253	8295	321	62	19	15	7	4	3	2	2	2	1

Table 2

Number of sharks discarded (by fishing gear and per area) from observations onboard fishing vessels and from interviews with fishermen at landing sites throughout the Mediterranean Sea during 1998–99. Area numbers: 1=Alboran Sea, 2=Balearic Islands area, 3=Catalonian Sea, 4=Tyrrhenian Sea, 5=Straits of Sicily, 6=Adriatic Sea, 7=Ionian Sea, 8=Aegean Sea, and 9=Levantine basin). Gear abbreviations: SWO-LL=swordfish longline, ABL-LL=albacore longline, BFT-LL=bluefin tuna longline, DN=driftnet, SO-LL_A=American-type swordfish longline.

	Onboard sampling (693 sharks) Number of discarded sharks						At landing sampling (8040 sharks) Number of discarded sharks reported				
Area	Sets observed onboard	SWO-LL	ALB-LL	BFT-LL	DN	SWO-LL_A	Sets observed at landings	SWO-LL	ALB-LL	BFT-LL	DN	SWO-LL_A
1	70	0	—	—	—	—	1321	0	—	—	—	—
2	192	0	0	0	—	—	1187	0	—	—	—	—
3	56	0	0	—	—	—	275	0	—	—	—	—
4	9	0	—	—	—	—	0	—	—	—	—	—
5	32	0	0	0	—	—	0	—	—	—	—	—
6	75	0	0	—	—	—	702	0	—	—	—	—
7	217	0	0	—	0	—	1331	0	0	—	0	—
8	39	0	—	—	—	7	102	0	0	—	—	0
9	12	0	—	—	—	0	206	0	—	—	—	0
Total	702	0	0	0	0	7	5124	0	0	—	0	0

6.2% in number and 13.5% in biomass of the catch sampled in swordfish and tuna fisheries. Sharks were rarely discarded from vessels and the rare instances were recorded only from areas off Greece. Out of 78 shark specimens caught by the Greek longline fishing vessels only seven blue sharks, killed onboard before they were unhooked, were thrown back to the sea. No shark discarding at sea was reported by the skippers of the fishing boats, nor by the fishermen interviewed at landing sites (Table 2). Fishermen usually do not discard their shark catch because there is a market demand for sharks in the Mediterranean countries. Twelve shark species were identified—blue shark (*Prionace glauca*), being the most common in all areas and gears studied.

Table 3

Biomass (in kg) and percentage composition of species sampled on selected vessels observed at-sea and as reported at landing sites, by fishing gear in the large pelagic fisheries of the Mediterranean Sea during 1998–99. Gear abbreviations: SWO-LL=swordfish longline, SWO-LL_A=American-type swordfish longline, ABL-LL=albacore longline, BFT-LL=bluefin tuna longline, DN=driftnet.

	SWO-LL		SWO-LL_A		ALB-LL		BFT-LL		DN		Total	
Species	kg	%	kg	%	kg	%	kg	%	kg	%	kg	%
At landing sites												
Sharks	139,056	19.01	1004	1.86	399	0.37	—	—	11,099	11.25	151,558	15.29
Swordfish	551,998	75.46	42,597	78.94	32,573	30.47	—	—	49,226	49.91	676,394	68.25
Bluefin tuna	17,511	2.39	9496	17.60	4500	4.21	—	—	31,224	31.66	62,731	6.33
Albacore	527	0.07	192	0.36	65,149	60.95	—	—	7085	7.18	72,953	7.36
Other	22,457	3.07	675	1.25	4266	3.99	—	—	—[1]	—[1]	27,398	2.76
Total	731,549		53,964		106,887		—	—	98,634		991,034	
On board												
Sharks	11,793	9.64	785	8.08	267	0.26	297	2.10	258	14.45	13,400	5.33
Swordfish	82,885	67.77	7146	73.57	5259	5.07	192	1.36	1486	83.22	96,969	38.54
Bluefin tuna	2981	2.44	1617	16.65	13,474	13.00	13,459	94.99	42	2.33	31,572	12.55
Albacore	55	0.05	23	0.24	79,107	76.32	0	0.00	0	0.00	79,185	31.47
Other	24,584	20.10	142	1.46	5546	5.35	221	1.56	—[1]	—[1]	30,493	12.12
Total	122,298		9713		103,653		14,169		1786		251,619	
All												
Sharks	150,849	17.67	1789	2.81	666	0.32	297	2.10	11,357	11.31	164,958	13.27
Swordfish	634,884	74.37	49,743	78.12	37,833	17.97	192	1.36	50,712	50.50	773,364	62.23
Bluefin tuna	20,492	2.40	11,113	17.45	17,974	8.54	13,459	94.99	31,266	31.13	94,303	7.59
Albacore	582	0.07	215	0.34	144,255	68.52	0	0.00	7085	7.06	152,138	12.24
Other	47,041	5.51	817	1.28	9812	4.66	221	1.56	—[1]	—[1]	57,891	4.66
Total	853,848		63,677		210,540		14,169		100,420		1,242,654	

[1] No weight data were available for other species.

Shortfin mako (*Isurus oxyrinchus*), common thresher shark (*Alopias vulpinus*), and tope shark (*Galeorhinus galeus*) were the next most abundant shark species and were found in more than half of the areas sampled. The rest of the shark species identified were the porbeagle (*Lamna nasus*), bigeyed thresher shark (*Alopias superciliosus*), smooth hammerhead (*Sphyrna zygaena*), bluntnose sixgill shark (*Hexanchus griseus*), sandbar shark (*Carcharinus plumbeus*), longnose spurdog (*Squalus blainvillei*), smoothhound (*Mustelus mustelus*), and basking shark (*Cetorhinus maximus*).

The proportions of shark catches were significantly different among fishing gears (χ^2=15970.7, df=36, P=0.000<0.001). Total shark catches in biomass represented 17.7% on swordfish longline gear, 11.3% on driftnet gear, and only 0.3% on albacore longline gear (Table 3). Comparisons of catch composition among the fishing gears in the same area showed similar results. In the Ionian Sea, shark percentage was higher in the swordfish longline catch than in the driftnet and albacore longline catch (Table 4). Catch composition also differed significantly by area (χ^2=494558.4, df=112, P=0.000<0.001). The higher percentage of sharks, 34.3%, was found in the Alboran Sea and the lower percentages, in the Straits of Sicily and the Catalonian Sea (Table 5). Statistically highly significant differences were detected in catch composition among types of sampling (χ^2=29760.41, df=17, P=0.000<0.001). In all fishing gears and areas examined throughout the Mediterranean Sea, sharks represented 15.3% of the total catch in biomass at landings and only 5.3% onboard vessels. Among areas sampled, three areas (the Alboran Sea, Catalonin Sea, and Balearic Island area) revealed higher shark percentages at landing sites than onboard vessels (Table 5).

Relative shark abundance varied between fisheries. Higher shark catch rates were observed in swordfish fisheries both onboard vessels and at landing sites (Table 6 and 7). Overall CPUE reached 1.30 and 0.56 fish/1000 hooks in SWO-LL and SWO-LL_A, respectively (Table 8). Shark catch rates were higher in the Alboran Sea and the Adriatic Sea, where the average CPUEs were 3.80 fish/1000 hooks and 1 fish/1000 hooks, respectively in SWO-LL (Table 8). The driftnet fishery had a catch rate of only 0.04 fish/1000 m of nets. The comparison of catch rates (number of shark per set) among the different gear types in the same area (the Ionian Sea) revealed that the highest CPUE values were

Table 4

Biomass (in kg) and percentage composition of species by fishing gear sampled on selected vessels observed at-sea and as reported at landing sites in the Ionian Sea during 1998–99. Gear abbreviations: SWO-LL=swordfish longline, ABL-LL=albacore longline, DN=driftnet.

	SWO-LL		ALB-LL		DN		Total	
Species	kg	%	kg	%	kg	%	kg	%
Sharks	9787	13.4	568	0.5	11,357	11.3	21,711	7.5
Swordfish	43,395	59.5	35,122	30.6	50,713	50.5	129,229	44.9
Bluefin tuna	5838	8.0	5127	4.5	31,266	31.1	42,231	14.7
Albacore	0	0.0	67,594	58.9	7085	7.1	74,680	25.9
Other	13,921	19.1	6298	5.5	—[1]	—[1]	20,219	7.0
Total	72,941	100.0	114,709	100.0	100,421	100.0	288,070	100.0

[1] No available weight data were available for other species.

Table 5

Biomass (%) by species and area from data collected at landing sites and from selected longline vessels observed at-sea in the Mediterranean Sea during 1998–99. Area numbers: 1=Alboran Sea, 2=Balearic Islands area, 3=Catalonian Sea, 4=Tyrrhenian Sea, 5=Straits of Sicily, 6=Adriatic Sea, 7=Ionian Sea, 8=Aegean Sea, and 9=Levantine basin. Other = other species.

	Areas									
Species	1	2	3	4	5	6	7	8	9	Total
At landing sites										
Sharks	35.74	2.06	1.78	—	—	14.32	7.03	0.25	1.87	15.29
Swordfish	61.77	93.24	97.80	—	—	78.24	45.68	2.68	79.12	68.25
Bluefin tuna	1.83	1.89	0.28	—	—	2.62	16.12	3.39	17.42	6.33
Albacore	0.07	0.18	0.01	—	—	0.00	26.15	87.86	0.35	7.36
Other	0.59	2.62	0.13	—	—	4.82	5.02	5.82	1.24	2.76
Aboard longline vessels										
Sharks	7.82	1.14	0.78	5.63	0.89	19.57	10.69	11.18	2.89	5.33
Swordfish	81.04	38.15	12.91	42.66	31.73	44.40	39.73	81.31	60.60	38.54
Bluefin tuna	0.06	19.24	19.02	0.00	3.93	3.99	5.49	5.72	34.97	12.55
Albacore	0.00	33.91	67.06	0.00	44.44	4.34	24.53	0.28	0.17	31.47
Other	11.08	7.56	0.24	51.71	19.01	27.70	19.56	1.51	1.38	12.12
All										
Sharks	34.34	1.74	1.35	5.63	0.89	15.11	5.52	4.88	1.93	13.45
Swordfish	62.74	73.95	61.09	42.66	31.73	73.16	41.84	35.97	77.97	63.27
Bluefin tuna	1.74	7.97	8.38	0.00	3.93	2.83	5.84	4.38	18.52	5.52
Albacore	0.07	11.99	29.01	0.00	44.44	0.65	36.02	50.79	0.34	12.70
Other	1.11	4.35	0.18	51.71	19.01	8.25	10.77	3.99	1.25	5.07

found in the swordfish longline, about 1.02 fish/fishing set, followed by the driftnet and the albacore longline CPUE values (Table 9).

Seasonality in catch rates was evident in the swordfish longline fishery; shark CPUE peaked during late spring and summer, whereas swordfish CPUE peaked during fall and winter (Fig. 2). In the driftnet fishery, shark CPUE peaked during June and swordfish CPUEs were higher during June and July (Fig. 3).

Blue shark was the most abundant shark species in all areas and gears examined. It accounted for almost 95% of all sharks caught. Higher catch rates were observed in the swordfish fishery with an average value of 1.24 fish/1000 hooks in SWO-LL and 0.45 fish/1000 hooks in SWO-LL_A fishery. Analysis of catch rates by area showed that blue shark was caught more frequently in the Alboran and Adriatic Sea, reaching 3.59 fish/1000 hooks and 1.00 fish/1000 hooks, respectively (Table 8).

Table 6

Fishing sets, effort (×1000 hooks or 1000 m of net) and catch rates (number of fish/1000 hooks or number of fish/1000 m of net) of sharks and target species sampled on board in the large pelagic fisheries of the Mediterranean Sea during 1998–99. Gear abbreviations: SWO-LL=swordfish longline, SWO-LL_A=American-type swordfish longline, ABL-LL=albacore longline, BFT-LL=bluefin tuna longline, DN=driftnet. Abbreviations for species: PG=*Prionace glauca*, IO=*Isurus oxyrinchus*, AV=*Alopias vulpinus*, GG=*Galeorhinus galeus*. Target species for specific gears: *Xiphias gladius* for SWO-LL, SWO-LL_A and DN; *Thunnus alalunga* for ALB-LL; and *Thunnus thynnus* for BFT-LL.

				Catch rate						
Fishing gear	Area	Sets	Effort	PG	IO	AV	GG	Other sharks	Total sharks	Target species
SWO-LL	Ionian	140	267.4	0.759	0.000	0.000	0.000	0.004	0.763	3.152
	Adriatic	69	166.3	1.678	0.000	0.048	0.000	0.000	1.726	3.879
	Tyrrhenian	9	18.5	0.270	0.000	0.000	0.000	0.000	0.270	8.428
	Strait of Sicily	23	46.4	0.065	0.000	0.022	0.022	0.108	0.216	14.526
	Balearic	125	373.1	0.027	0.029	0.008	0.005	0.003	0.072	8.003
	Alboran	70	174.4	0.304	0.092	0.011	0.000	0.000	0.407	5.860
	Catalonian	15	43.5	0.299	0.023	0.023	0.023	0.046	0.414	6.989
	Total	451	1089.6	0.519	0.026	0.014	0.004	0.008	0.571	6.085
SWO-LL_A	Aegean	39	17.4	1.264	0.000	0.057	0.057	0.000	1.379	11.609
	Levantine	12	4.8	0.417	0.208	0.000	0.000	0.000	0.625	14.167
	Total	51	22.2	1.081	0.045	0.045	0.045	0.000	1.216	12.162
ALB-LL	Adriatic	6	15.3	0.000	0.000	0.000	0.000	0.000	0.000	22.222
	Ionian	47	112.9	0.168	0.000	0.000	0.000	0.000	0.168	13.853
	Strait of Sicily	7	17.5	0.000	0.000	0.000	0.000	0.000	0.000	127.143
	Balearic	48	158.7	0.000	0.006	0.000	0.000	0.006	0.013	23.732
	Catalonian	41	142.1	0.070	0.007	0.000	0.000	0.000	0.077	29.141
	Total	149	446.5	0.065	0.004	0.000	0.000	0.000	0.069	26.957
BFT-LL	Strait of Sicily	2	2.8	0.000	0.000	0.000	0.000	0.000	0.000	5.357
	Balearic	19	20.9	0.287	0.000	0.000	0.000	0.000	0.287	3.876
	Total	21	23.7	0.253	0.000	0.000	0.000	0.000	0.253	4.051
DN	Ionian	30	300.5	0.023	0.000	0.000	0.000	0.000	0.023	0.206

Of the 3771 blue sharks measured, individuals ranged from 40 to 368 cm TL (163.3 cm mean length and 37.7 cm SD). The overall length-frequency distribution is shown in Figure 4. The size distribution by fishing gear varied significantly (Kruskall-Wallis, test statistic=350.2, P=0.000<0.05); larger specimens were caught in the SWO-LL_A and DN fishery (Fig. 5). The Levantine basin had larger individuals whereas the Catalonian Sea had smaller ones (Fig. 6). Out of 564 blue sharks, 346 were determined to be males and 218 to be females. The sex ratio (males:female) favored males in almost all areas ranging from 1.29–2.50 males:1 female. The only exception was in the Alboran Sea where females were predominant (0.61 males:1 female). Relationships between TL and FL and dressed weight are given below:

$$TL = 4.1+1.176\ FL \qquad [r^2=0.99,\ n=723]$$
$$TL = 74.6\ DW^{0.307} \qquad [r^2=0.95,\ n=555].$$

The shortfin mako was reported in five out of nine areas examined and represented 3.7% of the overall shark catches. This species was caught more often in the swordfish fishery with a mean CPUE of 0.07 fish/1000 hooks in SWO-LL_A and 0.05 fish/1000 hooks in SWO-LL. Shortfin makos were more abundant in the Alboran Sea and the Levantine basin (Table 8).

The total length-frequency distribution for the 257 specimens measured is shown in Figure 4. For shortfin makos collected, almost all were juvenile and ranged from 62.5 cm to 272 cm TL (mean length of 120.6 cm and 30.9 cm SD). Each fishing gear caught a statistically significant different average TL size (Kruskall-Wallis, test statistic=23.8, P=0.000006<0.05), and larger specimens were observed in the SWO-LL_A fishery (Fig. 5). As with the blue shark, larger makos came from the Levantine basin and smaller ones from the Catalonian Sea (Fig. 6). Out of 56 shortfin makos, 27 were determined to be males and 29 to be females. Sex ratio was almost equal (0.9 male:1 female). The relationship between FL and TL is given below:

$$TL = 1.136\ FL - 2.5 \qquad [r^2=0.98,\ n=49].$$

Table 7

Fishing sets, effort (×1000 hooks or 1000 m of net) and catch rates (number of fish/1000 hooks or number of fish/1000 m of net) of sharks and target species sampled in the large pelagic fisheries of the Mediterranean Sea during 1998–99 as reported at landing sites. Gear abbreviations: SWO-LL=swordfish longline, SWO-LL_A=American-type swordfish longline, ABL-LL= albacore longline, DN=driftnet. Abbreviations for species: PG=*Prionace glauca*, IO=*Isurus oxyrinchus*, AV=*Alopias vulpinus*, GG=*Galeorhinus galeus*. The target species for specific gears: *Xiphias gladius* for SWO-LL, SWO-LL_A and DN; *Thunnus alalunga* for ALB-LL.

				Catch rate						
Fishing gear	Area	Sets	Effort	PG	IO	AV	GG	Other sharks	Total sharks	Target species
SWO-LL	Ionian	454	883.5	0.457	0.000	0.001	0.000	0.002	0.461	2.521
	Levantine	7	7.0	0.000	0.000	0.000	0.143	0.000	0.143	7.714
	Adriatic	702	1895.3	0.936	0.000	0.000	0.000	0.001	0.937	3.562
	Balearic	1187	795.7	0.087	0.038	0.018	0.003	0.000	0.145	15.474
	Alboran	1321	1232.3	4.061	0.204	0.007	0.008	0.005	4.285	11.259
	Catalonian	275	478.6	0.155	0.002	0.002	0.002	0.000	0.161	5.894
	Total	3946	5292.4	1.384	0.053	0.005	0.003	0.001	1.445	7.188
SWO-LL_A	Aegean	3	1.1	0.000	0.000	0.000	0.000	0.000	0.000	5.714
	Levantine	199	90.1	0.300	0.078	0.011	0.000	0.011	0.400	15.461
	Total	202	91.2	0.296	0.077	0.011	0.000	0.011	0.395	15.348
ALB-LL	Aegean	99	151.0	0.040	0.000	0.000	0.000	0.000	0.040	5.589
	Ionian	192	414.1	0.075	0.000	0.000	0.000	0.000	0.075	21.166
	Total	291	565.1	0.065	0.000	0.000	0.000	0.000	0.065	15.868
DN	Ionian	685	8035.8	0.034	0.000	0.002	0.000	0.001	0.038	0.215

Common thresher shark, the third most abundant shark reported in eight out of nine areas studied, accounted for 0.74% of the total shark catches. Catch rates per fishing gear were higher in the SWO-LL_A fishery with a mean CPUE of 0.02 fish/1000 hooks and per area sampled in the Aegean Sea, reaching 0.05 fish/1000 hooks (Table 8).

A total of 48 juvenile and adult common thresher sharks were measured. Length-frequency distribution was discontinuous and not very revealing because of the small number of sharks sampled (Fig. 4). Specimens ranged from 75 to 514 cm TL (mean value of 316.8 cm and SD 86.4 cm). No statistically significant differences were observed (Kruskall-Wallis, test statistic=0.638, P=0.73>0.05) in average size of specimens by fishing gear (Fig. 5). Larger specimens were reported from the Levantine basin area and a smaller one was reported from the Balearic Sea (Fig. 6). Out of 27 common thresher shark sexed, 15 were males and 12 females. Sex ratio was 1.25 male:1 female. The TL-FL and TL-dressed weight relationships are given below:

$$TL = 20.2 + 1.707\ FL \qquad [r^2=0.95,\ n=24]$$
$$TL = 69.7\ DW^{0.351} \qquad [r^2=0.99,\ n=18].$$

The remaining nine shark species observed accounted for only 0.87% of the total shark catches. In total, 26 tope sharks were measured (ranging from 35 to 190 cm), 15 porbeagles (ranging from 87 to 277 cm), 7 bigeyed thresher sharks (ranging from 146 to 353 cm) and 4 smooth hammerheads (ranging from 277 to 300 cm TL). Only three bluntnose sixgill sharks (mean weight of 10.7 kg), two sandbar sharks (mean weight of 17 kg), two longnose spurdogs (mean weight of 1.7 kg), two basking sharks, and one smoothhound were reported, but no length measurements were available for these species.

A total of 571 specimens were examined for life condition on capture. The majority were very active following capture and their physical condition was especially good. Only 5.1% of the specimens brought onboard were dead (Table 10).

Discussion

Our results show that most of the sharks caught by the swordfish and tuna fisheries in the Mediterranean Sea are typically pelagic or coastal-pelagic species of widespread distribution in temperate and tropical waters throughout the world. However, some sporadic catches of poorly known, deepwater species of the families Hexanchidae and Alopiidae were also observed. The most plausible reason for these catches is that the deepwater species ascend close to the surface at night where they may be taken by longlines targeting swordfish (Castro et al., 1999).

Table 8

Fishing sets, effort (×1000 hooks or 1000 m of net), and catch rates (number of fish/1000 hooks or number of fish/1000 m of net) of sharks and target species sampled in the large pelagic fisheries of the Mediterranean Sea during 1998–99. Sampling conducted both at sea and at landing sites. PG=*Prionace glauca*, IO=*Isurus oxyrinchus*, AV=*Alopias vulpinus*, GG=*Galeorhinus galeus*. The target species for specific gears: *Xiphias gladius* for SWO-LL, SWO-LL$_A$ and DN; *Thunnus alalunga* for ALB-LL; and *Thunnus thynnus* for BFT-LL.

				Catch rate						
Fishing gear	Area	Sets	Effort	PG	IO	AV	GG	Other sharks	Total sharks	Target species
SWO-LL	Ionian	594	1151.0	0.53	0.00	0.001	0.00	0.003	0.53	2.67
	Levantine	7	7.0	0.00	0.00	0.00	0.14	0.00	0.14	7.71
	Adriatic	771	2061.6	1.00	0.00	0.004	0.00	0.00	1.00	3.59
	Tyrrhenian	9	18.5	0.27	0.00	0.00	0.00	0.00	0.27	8.43
	Strait of Sicily	23	46.4	0.06	0.00	0.02	0.02	0.11	0.22	14.53
	Balearic	1312	1168.8	0.07	0.04	0.01	0.003	0.001	0.12	13.09
	Alboran	1391	1406.7	3.59	0.19	0.008	0.007	0.004	3.80	10.59
	Catalonian	290	522.1	0.17	0.004	0.004	0.004	0.004	0.18	5.99
	Total	4397	6382.0	1.24	0.05	0.006	0.003	0.002	1.30	7.00
SWO-LL$_A$	Aegean	42	18.5	1.19	0.00	0.05	0.05	0.00	1.30	11.27
	Levantine	211	94.9	0.31	0.08	0.01	0.00	0.01	0.41	15.40
	Total	253	113.4	0.45	0.07	0.02	0.01	0.01	0.56	14.72
ALB-LL	Aegean	99	151.0	0.04	0.00	0.00	0.00	0.00	0.04	5.59
	Adriatic	6	15.3	0.00	0.00	0.00	0.00	0.00	0.00	22.22
	Ionian	239	527.0	0.09	0.00	0.00	0.00	0.00	0.09	19.60
	Strait of Sicily	7	17.5	0.00	0.00	0.00	0.00	0.00	0.00	127.14
	Balearic	48	158.7	0.00	0.006	0.00	0.00	0.006	0.013	23.73
	Catalonian	41	142.1	0.07	0.007	0.00	0.00	0.00	0.08	29.14
	Total	440	1011.6	0.07	0.002	0.00	0.00	0.00	0.07	20.76
BFT-LL	Strait of Sicily	2	2.8	0.00	0.00	0.00	0.00	0.00	0.00	5.36
	Balearic	19	20.9	0.29	0.00	0.00	0.00	0.00	0.29	3.88
	Total	21	23.7	0.25	0.00	0.00	0.00	0.00	0.25	4.05
DN	Ionian	715	8336.3	0.03	0.00	0.002	0.00	0.001	0.04	0.21

Table 9

Fishing sets and catch rates (number of fish/fishing set) of sharks and target species in the three fishing gears studied in the Ionian Sea during 1998–99. PG=*Prionace glauca*, IO=*Isurus oxyrinchus*, AV=*Alopias vulpinus*, GG=*Galeorhinus galeus*. The target species for specific gears: *Xiphias gladius* for SWO-LL and DN; *Thunnus alalunga* for ALB-LL.

		Catch rate						
Fishing gear	Sets	PG	IO	AV	GG	Other sharks	Total sharks	Target species
SWO-LL	594	1.02	0.00	0.00	0.00	0.01	1.03	5.17
ALB-LL	239	0.21	0.00	0.00	0.00	0.00	0.21	43.22
DN	715	0.39	0.00	0.03	0.00	0.02	0.44	2.50

Onboard observations and interviews with fishermen at landing sites revealed that shark discarding is not a common practice in the large pelagic fisheries in the Mediterranean Sea. Very few shark discards were recorded and only from Greek vessels (seven blue sharks out of 78 total). The fishermen usually retain their incidental catches because there is a market demand for sharks in Europe. However, wholesale shark flesh prices are quite variable, ranging from 2 to 8 euros. Moreover, the jaws and tails of some shark species are often sold

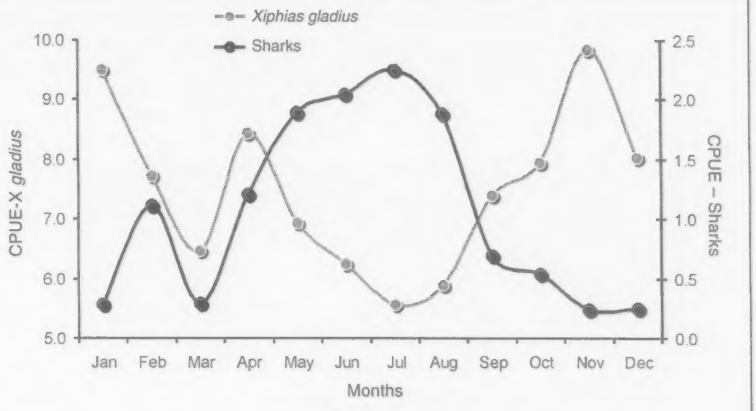

Figure 2

Monthly variation in sharks and swordfish longline CPUE (catch in numbers/1000 hooks) in the swordfish longline fishery of the Mediterranean Sea during 1998–99.

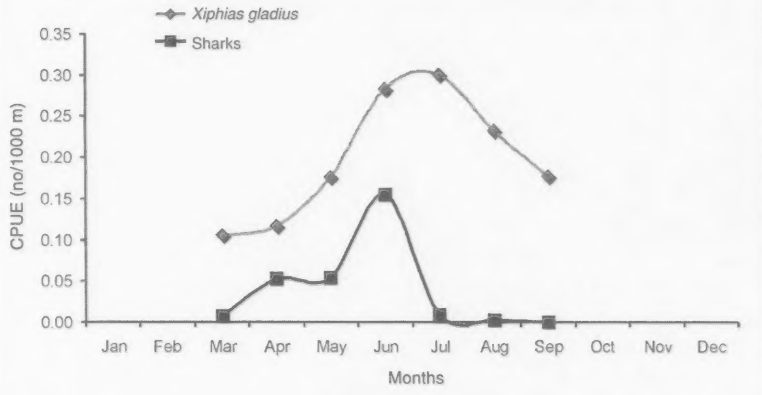

Figure 3

Monthly variation in sharks and swordfish CPUE (catch in numbers/1000 m net) in the driftnet fishery of the Mediterranean Sea during 1998–99.

in local markets. The very low discard rate of shark—about 1% of the sharks caught during onboard sampling was discarded—confirmed that sharks contribute to fishermen's income and may become target species with future increases in their market value. That discarding was observed only in the Greek swordfish fleets is probably due to the low market prices of shark meat compared to the high price of swordfish in this country. Sometimes during long trips fishermen are reluctant to retain them onboard and loose cool storage space for more valuable species such as swordfish or tuna.

The analysis of catch composition by gear and areas indicated that the various gears used in the swordfish and tuna fisheries affect the shark populations differently and that the proportion of shark catches is related both to the type of fishing gear and the sampling area. This finding is consistent with previous findings for the Mediterranean Sea where incidental shark catch in the swordfish fisheries varied from insignificant to dominant, depending on the area studied (De Metrio et al., 1984; Di Natale, 1998; Filanti et al., 1986; Buencuerpo et al., 1998; Mejuto et. al., 2002). The highest shark incidental catches were found in the Alboran Sea and were probably related to their location (Alboran Sea), adjacent to the Atlantic Ocean. Shark bycatch in the Atlantic swordfish fishery is one

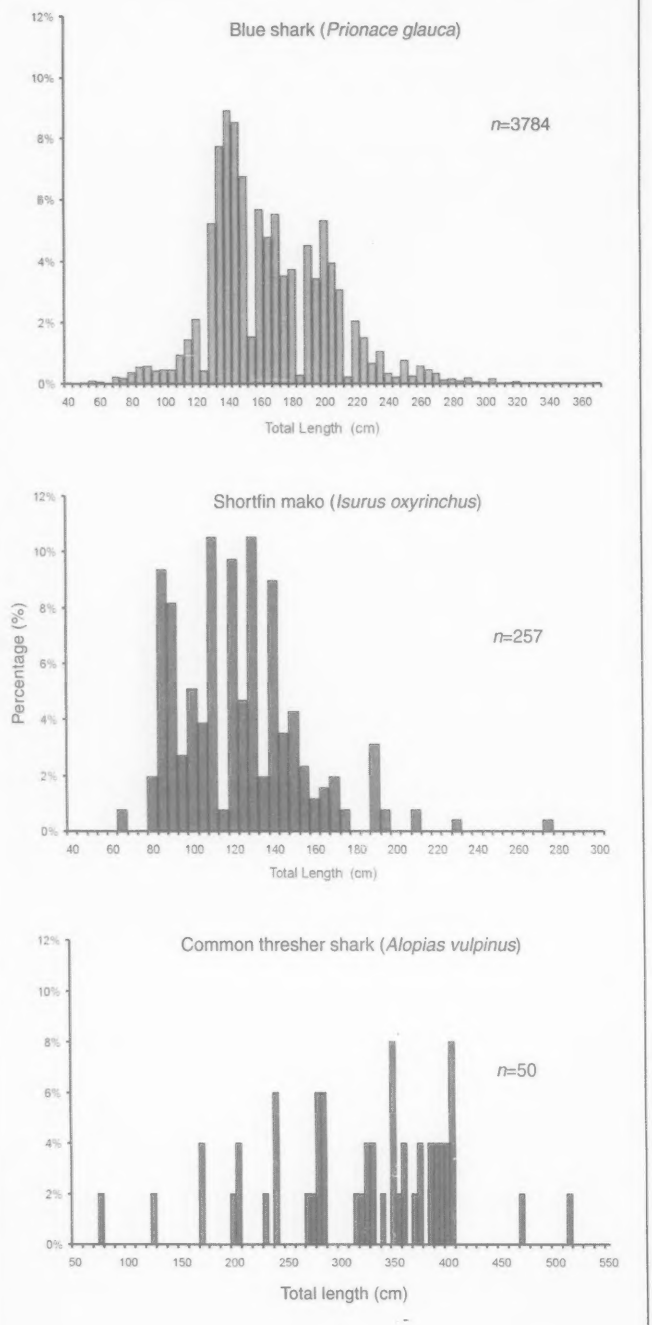

Figure 4

Length-frequency distribution (in percentage by 5-cm size classes) for *Prionace glauca*, *Isurus oxyrinchus*, and *Alopias vulpinus* sampled in the Mediterranean Sea during 1998–2000.

of the highest in the world, rarely dropping below 30% of the total catch in numbers of fish (Amorim et al., 1998; Buencuerpo et al., 1998; Hazin et al., 1998; Marin et al., 1998). The higher incidence of sharks in the Alboran Sea could also be due to the higher trophic potential of the western Mediterranean compared to the eastern part. The discrepancies in observed at-sea and at-landing data, especially in the western Mediterranean Sea catch composition, could be mainly due to the discarding of "other species." In addition, the discarding of undersize target species, such as swordfish and tunas, could be another reason for the discrepancies observed. It is reasonable that observers at landing sites were not able to record exactly the entire nonshark discards at sea from the information that fishermen provided; thus shark landings do not always reflect actual percentage of catch composition caught at sea.

The shark catch rates obtained in our study were lower than those reported in previous studies for various areas of the Mediterranean Sea (Table 11) probably because of the fishing pressure throughout the years.

A comparison of the shark catch rates in the Mediterranean and Atlantic indicated that the catch rates are generally lower throughout the Mediterranean (Table 11). Possible reasons could be either the lower productivity of the Mediterranean Sea, or, as alluded to above, lower availability of sharks in the Mediterranean due to regional depletion from historical fishing, or both. The configuration and effectiveness of fishing gears used could be another reason for the higher CPUE in the Atlantic Ocean. Hazin et al. (1998) and Kotas et al.[2] reported an increase in use of wire snoods in Atlantic swordfish fisheries to retain more sharks for the growing market for shark fins.

Monthly analysis of catches indicated that maximum catch rates occur during late spring and summer (May–August) in the swordfish longline (SWO-LL) fishery, and in June in the driftnet fishery. Monthly variations in catch rates were found also by Buencuerpo et al. (1998), who reported peaks of shark catch in April and Septem-

[2] Kotas, J. E., S. dos Santos, V. G. de Azevedo, J. H. de Lima, J. D. Neto, and C. F. Lin. 2000. Observations on shark by-catch in the monofilament longline fishery off southern Brazil and the National ban on finning, 8 p. IBAMA–REVIZEE research. [Copyright: www.wildaid.org.]

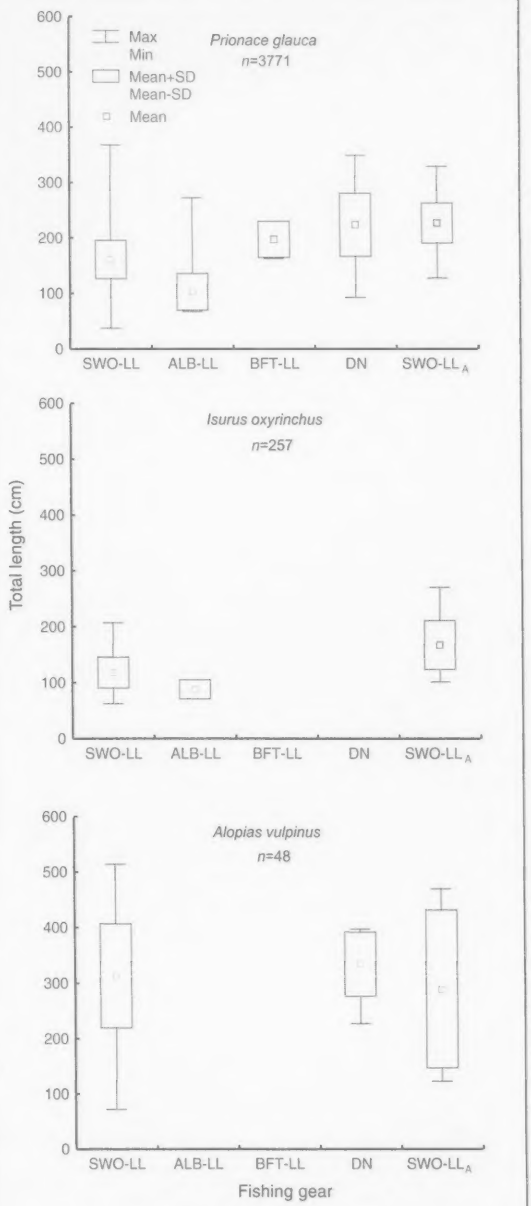

Figure 5

Size-range variation for *Prionace glauca*, *Isurus oxyrinchus*, and *Alopias vulpinus* by fishing gear in the Mediterranean Sea during 1998–2000. See Table 1 for definitions of abbreviations for fishing gear along *x* axis.

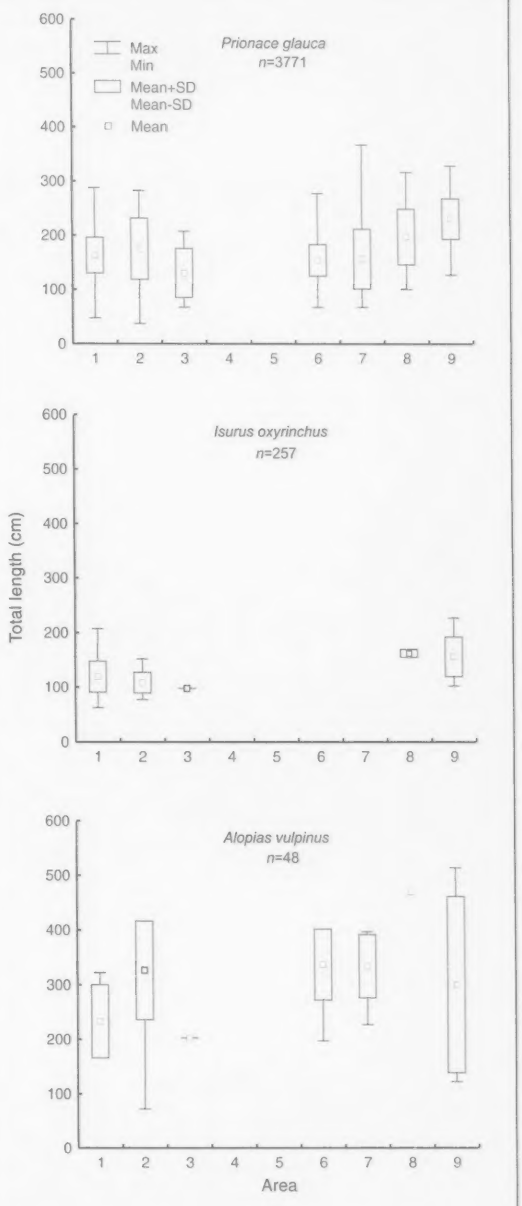

Figure 6

Size-range variation for *Prionace glauca*, *Isurus oxyrinchus*, and *Alopias vulpinus* by area sampled in the Mediterranean Sea during 1998–2000. See Table 1 for definitions of area numbers along the *x* axis.

ber in the eastern N. Atlantic and Straits of Gibraltar. Probably, certain water temperature preferences of sharks during their biological cycle force them to shift to shallower and warmer water masses, especially in summer. At these depths sharks are more vulnerable to surface gears and that is reflected in higher catches. Higher catch rates in late spring and summer could be also attributed to juvenile recruitment (Strasburg,

Table 10

Life-status condition of 571 sharks at time of capture, by species, and per fishing gear, observed onboard commercial fishing vessels in the Mediterranean Sea during 1998–2000. Gear abbreviations: SWO-LL=swordfish longline, SWO-LL_A=American-type swordfish longline, ABL-LL=albacore longline, DN=driftnet, BFT-LL=bluefin tuna longline.

	Good		Fair		Poor		Dead	
	Number	%	Number	%	Number	%	Number	%
Species								
P. glauca	364	71.0	69	13.5	57	11.1	23	4.5
I. oxyrinchus	7	22.6	10	32.3	9	29.0	5	16.1
A. vulpinus	3	18.8	4	25.0	8	50.0	1	6.3
G. galeus	4	80.0	1	20.0	0	0.0	0	0.0
A. superciliosus	1	100.0	0	0.0	0	0.0	0	0.0
C. plumbeus	0	0.0	2	100.0	0	0.0	0	0.0
H. griseus	3	100.0	0	0.0	0	0.0	0	0.0
Fishing gear								
SWO-LL	334	66.8	76	15.2	64	12.8	26	5.2
SWO-LL_A	34	97.1	0	0.0	0	0.0	1	2.9
ALB-LL	12	46.2	6	23.1	6	23.1	2	7.7
DN	2	40.0	2	40.0	1	20.0	0	0.0
BFT-LL	0	0.0	2	40.0	3	60.0	0	0.0
Total	382	66.9	86	15.1	74	13.0	29	5.1

1958; Carey and Scharold, 1990; Nakano, 1994; Bigelow et al., 1999).

The abundance and widespread distribution of blue sharks throughout the Mediterranean that we determined supports previous findings. However, our observed catch rates were lower than those reported earlier for the same areas (De Metrio et al., 1984; Filanti et al., 1986; Buencuerpo et al., 1998; Di Natale, 1998; Relini-Orsi et al., 1999; De Zio et al., 2000). Variation in sex ratio and size distribution between different areas studied indicated sexual or size segregation, or both. Spatial and temporal segregation of pelagic sharks by sex and size was well documented by Strasburg (1958) and Nakano (1994) in the Pacific Ocean. Further analysis regarding distribution by latitude-longitude, time of year, and size classes of specimens is needed to establish a possible blue shark migratory pattern in the Mediterranean Sea. Pratt's estimates on the sexual maturity of blue shark (215 cm TL for males, 257 cm TL for females) from the North Atlantic Ocean (Pratt, 1979) indicate that in all areas studied in the Mediterranean Sea, albacore and swordfish longline fisheries generally capture immature to subadult specimens and driftnets and American type swordfish longlines capture adults. Of all blue sharks captured in the large pelagic fisheries of the Mediterranean during our study, 91.1% were under 215 cm TL and 96.3% under 257 cm TL. This observation, which indicates that the majority of Mediterranean blue sharks caught have not reached maturity, is of concern and reinforces the need for global assessments of this species. In the Atlantic and Pacific Ocean results based on a considerable time series of data show a decrease in abundance (Cramer, 1996) and in average size (Holts et al., 1998) of blue sharks. Because blue sharks are an incidental catch in the large pelagic and highly migratory species fisheries in the Mediterranean, standardizing catch rates is very difficult. Average size may be a more sensitive indicator of shark stock status than catch rates when there is a long enough time-series of data.

We found a much lower incidental catch of shortfin mako than other authors have reported in the Mediterranean (Dai, 1997; Buencuerpo et al., 1998). This species seems more abundant in the Atlantic Ocean where in some areas it represents more than 10% of total catches (Buencuerpo et al., 1998; Stone et al., 2001). The almost equal sex ratio reflects the findings of Buencuerpo et al., (1998) and Moreno et al., (1992). As with blue sharks, larger makos were observed in the Levantine basin although in small numbers. Because males mature at 195 cm TL (Compagno, 1984) and females between 273 and 298 cm (Mollet et al., 2000), 98.4% of shortfin makos in our study were smaller than the size of first maturity. The absence of a consistent time series of abundance data did not allow us to estimate the trend in the status of the shortfin mako population in the Mediterranean Sea. Cramer (1996) outlined a steady decline in catch indices for this species from 11.86 fish/1000 hooks in 1985, to 3.52 in 1996 for the U.S. commercial Atlantic longline fishery in the Caribbean and the Gulf of Mexico. The Azorean fleet mako landings decreased by almost 50% in numbers from 1987 to 1994 (Castro et al., 1999). Together with the low catch rates in the Mediterranean Sea, short-

Table 11

Comparison of shark catch rates (CPUE in number of fish/1000 hooks) in longline fisheries during investigations in the Mediterranean Sea and the Atlantic Ocean. SWO-LL= swordfish longline; Tuna-LL=tuna longline gear.

Author	Area	Period	Gear	CPUE
De Metrio et al. (1984) [1]	Ionian Sea	1984	SWO-LL	0.9–2.2
Filanti et al.(1986)	Ionian Sea	1978–85	SWO-LL	1.5–3.0
De Zio et al. (2000)	Adriatic Sea	1984–98	SWO-LL	2.4
Di Natale (1998)	Tyrrhenian Sea, Strait of Sicily	1991–92	SWO-LL	0.4
Buencuerpo et al. (1998)	Gibraltar Strait	1991–92	SWO-LL	24.2
Present study	Ionian Sea	1998–99	SWO-LL	0.5
Present study	Adriatic Sea	1998–99	SWO-LL	1.0
Present study	Strait of Sicily	1998–99	SWO-LL	0.2
Present study	Alboran Sea	1998–99	SWO-LL	3.8
Buencuerpo et al. (1998)	E. Atlantic	1991–92	SWO-LL	9.9–37.8
Stone and Dixon (2001)	NW Atlantic	1999	SWO-LL	43.8
Hazin et al. (1998)	W. Atlantic	1983–97	Tuna-LL	16.8

[1] Blue shark catch rates only.

fin makos may be one of the most over-fished pelagic sharks in the Mediterranean Sea.

Our low catch rates for common thresher shark in the Mediterranean were almost identical with the findings of Buencuerpo et al. (1998) for the Gibraltar Strait region. However, the abundance of this species supports directed fisheries in some areas. Such a case occurred off California waters during 1977–85, when thresher shark CPUE in the driftnet fishery ranged from 0.13 to 1.92 fish/fishing set (Holts et al., 1998). In our study, one third of the specimens caught came from the Ionian driftnet fishery but the largest individual was captured in the Levantine basin (514 cm TL) with the swordfish longline. Pacific females mature at 315 cm TL (Strasburg, 1958) and males mature at about 333 cm TL (Cailliet and Bedford, 1983), and we calculated that 40% of the female common thresher sharks caught were below 315 cm and 50% of the males were below 333 cm. Although the above data indicate that most were caught as immature sharks, there are no data on the first maturity of common thresher sharks in the Mediterranean Sea. There is doubt, however, that females mature at a smaller size than males in the same region and we therefore deduced that fishing pressure was very intense on juvenile and subadult groups.

The low capture numbers for other shark species could be due either to the scarcity of these species in the Mediterranean Sea or to the "fished-down" condition of shark populations, or both could be causes. Another reason could be the low capture efficiency of the gears used.

The high proportion of sharks that were alive on capture agrees with Kotas et al.[2], who reported that 97% of blue sharks and 78% of shortfin makos were alive when landed on deck. These high survival rates are encouraging and could become the basis for conservation measures in the future, such as releasing immature fish or enforcing catch quotas.

Our study provides a reference point for the present status of pelagic sharks in the Mediterranean Sea, the effect of fisheries on them, and a baseline for future monitoring. Fishing for swordfish and tunas affects much of the pelagic ecosystem by taking predators of swordfish and tunas (large pelagic sharks), their prey (small tunas), and their competitors, such as other elasmobranchs, billfishes, and tunas. Up to now, there has been little documentation and understanding of fishing effects on the wider ecosystem. To strengthen management for large pelagic fishes such as sharks, a multispecies assessment with an ecosystem approach should be adopted. To achieve this goal, long-term monitoring programs should be established and exploitation strategies should be linked to conservation plans for shark species in the Mediterranean Sea.

Acknowledgments

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Reproductive biology of female Rikuzen sole (*Dexistes rikuzenius*)*

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Abstract—The annual ovarian cycle, mode of maturation, age at maturity, and potential fecundity of female Rikuzen sole (*Dexistes rikuzenius*) from the North Pacific Ocean off the coast of Japan were studied by 1) histological examination of the gonads, 2) measurement and observation of the oocytes, and 3) by otolith aging. The results indicated that ovulation occurs from September to December and peaks between September and October. Vitellogenesis began again soon after the end of the current season. Maturity was divided into eight phases on the basis of oocyte developmental stages. Mature ovaries contained developing oocytes and postovulatory follicles but no recruiting oocytes, indicating that this species has group-synchronous ovaries and is a multiple spawner. Almost all females matured first at an age of 1+ year and spawned every year until at least age 8+ years. Potential fecundity increased exponentially with body length and the most fecund fish had 15 times as many oocytes as the least fecund fish. Potential fecundity and relative fecundity were both positively correlated with age from 1 to 6+ years, but were negatively correlated, probably because of senescence, in fish over 7 years. These results emphasize that the total productivity of a *D. rikuzenius* population depends not only on the biomass of females older than 1+ but also on the age structure of the population.

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To understand fish population dynamics, reproductive information, such as the maturation of oocytes, the size and age at first maturity, and fecundity, is indispensable. Gonadal maturation is determined from the external appearance of the gonads, the gonadosomatic index, and oocyte size, or from observations of histologically prepared gonads (West, 1990). With the former two methods it is possible to measure samples in the field and to record data on numerous samples in a short period of time; however, the mode of oocyte development can only be clarified by using observations of histologically prepared gonads (Wallace and Selman, 1981). The methods used to determine if an individual has spawned and to measure the number of eggs spawned in the current reproductive season differ with the mode of oocyte development (West, 1990).

In fishery models, reproductive potentials are conventionally represented by spawning stock biomass (Ricker, 1954; Beverton and Holt, 1957; Trippel et al., 1997). However, at the population level spawning stock biomass does not always correlate with egg productivity. Length at first maturation, the frequency of occurrence of degenerated oocytes, and fecundity (that is, the total number of offspring produced in a reproductive season by an individual female) are closely related to the age and energetic conditions of an individual (Hunter and Macewicz, 1985a; Horwood et al., 1986, 1989; Trippel et al., 1997; Sampson and Al-Jufaily, 1999; Kurita et al., 2003). Therefore, examination of age and body size in relation to fecundity is useful in determining the abundance of eggs laid in a population.

Oocyte development can be divided into three types (Wallace and Selman, 1981). In determinate fecundity, fecundity is fixed before spawning starts, such as in species which have synchronous or group-synchronous ovaries. In indeterminate fecundity (i.e., for those species whose ovaries develop asynchronously), unyolked oocytes grow to maturity after the onset of spawning (Hunter and Macewicz, 1985b; Hunter et al., 1992). In addition, the development of oocytes can vary even among populations of a single species (Sampson and Al-Jufaily, 1999) and some females classified as maturing or mature by external observation are often actually immature, and vice versa (Hunter et al., 1992; Zimmermann, 1997). Hence, with a species or a population for

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which little information is available, it is important to determine specific reproductive traits by using the most accurate methods and to compare the results with those of simpler methods.

Rikuzen sole (*Dexistes rikuzenius*) (also known as Rikuzen flounder, FAO) is a coastal flatfish that lives at depths of 100 to 360 m in the waters off the south coast of southern Hokkaido, Japan, and the southern Korean Peninsula (Sakamoto, 1984). It inhabits sandy bottoms and preys mainly on benthic invertebrates (Fujita et al., 1995). It is relatively abundant in the North Pacific off the coast of Japan and is an important fishery resource for bottom trawlers (Ishito, 1964; Ogasawara and Kawasaki, 1980). The commercial catch of flatfish such as the Rikuzen sole has fluctuated widely in this area over the past few decades (Anonymous, 2002), and therefore fisheries management is needed to maintain stable and appropriate fish-density levels.

In addition to fisheries, various internal and external conditions may affect the fluctuations in abundance of fish populations. Understanding reproductive traits, or survival in the early life stages, is a step toward revealing population dynamics. Although both sexes have indeterminate growth trajectories, conspicuous sexual dimorphism occurs during the growth and life span of Rikuzen sole. Females are larger at any given time after age 1+ and live longer than males (Ishito, 1964). The spawning period of the Sendai Bay population occurs from late October to late January and peaks from November to December (Ogasawara and Kawasaki, 1980). Using measurements of oocyte diameter and the appearance of the whole ovary, Ogasawara and Kawasaki (1980) revealed that females spawn several batches of eggs during one spawning season. However, because histological observations of the gonads have not been conducted, details of the reproductive biology, such as annual cycle of oocyte development, and body size and age at maturity, have not been determined. In addition, no information about fecundity has been reported.

We examined the oogenesis of Rikuzen sole caught in the North Pacific Ocean off the coast of Japan over a period of one year. The aim was to determine the mode of maturation, annual reproductive cycle, and age at first maturity based on histological examinations, age determinations from otolith growth increments, and gonadosomatic indices (GSIs). Using these results, we were able to estimate body size and age-related potential fecundity and were able to develop a simpler method for determining potential fecundity.

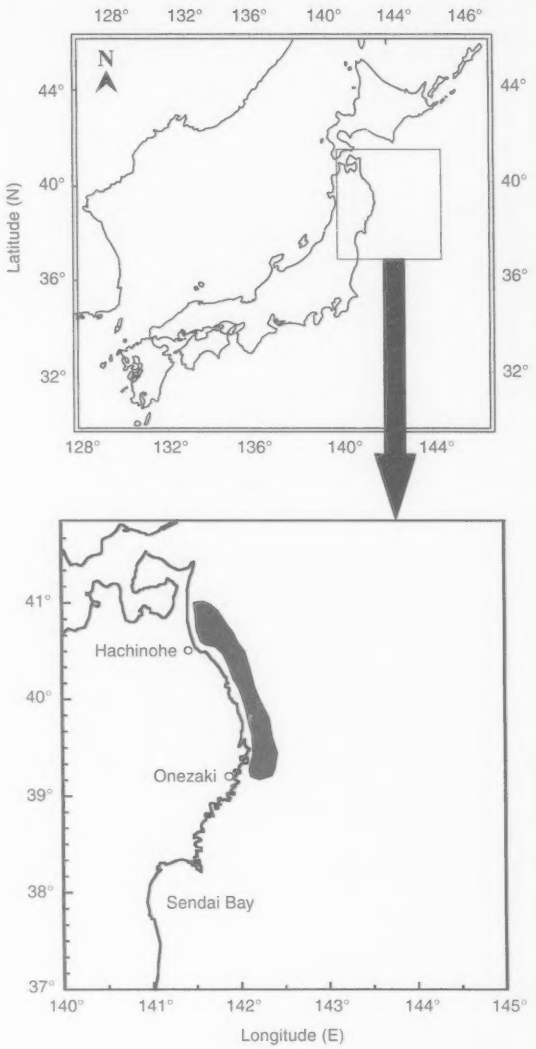

Figure 1

Catch area for Rikuzen sole (*Dexistes rikuzenius*) in the Northern Pacific Ocean off the northeast coast of Japan, 2000–2001.

Materials and methods

From May 2000 to April 2001, except for July and August when commercial bottom trawl fishing was prohibited, Rikuzen sole samples were collected once or twice a month from the fisheries market in Hachinohe, Aomori Prefecture, Japan. All samples were caught by bottom trawl nets in the coastal waters off Shitsukari (41°22′, 141°33′E) and Hachinohe (40°43′N, 144°44′E), from depths of 70–300 m (Fig. 1). During July and August, samples were collected with bottom long lines off the coast at Onezaki (39°12′N, 141°56′E) from a depth of 85–109 m.

A total of 1031 females were collected and their standard lengths (SL) to the nearest mm, total body weights, eviscerated body weights, and ovary weights to the nearest 0.1 g were measured. The GSI and body condition (BC) of each specimen were calculated with the following formulas: GSI = (*gonad weight/eviscerated body weight*)×100, and *BC* = (*eviscerated body weight/* SL^3)×100. Ovaries and sagittal otoliths were removed

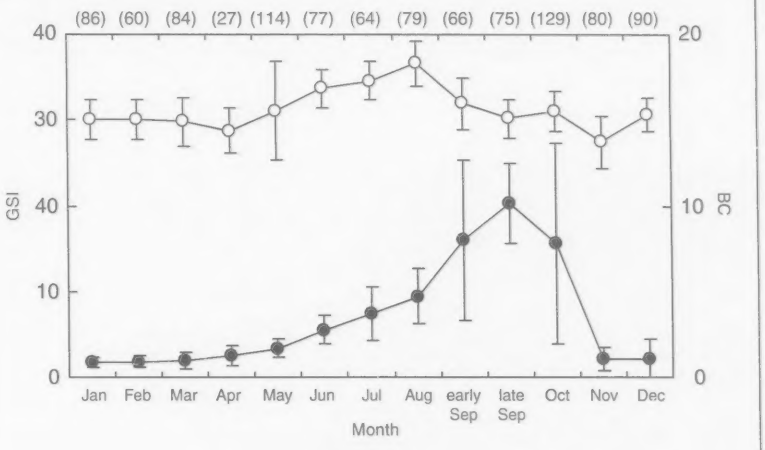

Figure 2

Annual changes in the gonadsomatic index (GSI) and body condition (BC) values of female Rikuzen sole (*Dexistes rikuzenius*). Solid and open circles show the mean values of GSI and BC, respectively. Vertical bars represent the standard deviations of these means. Sample numbers are shown in brackets.

within a day after each catch for histological observations and age determination, respectively. The otoliths were washed with distilled water and left to dry until preparation for age determination. Ovaries were fixed in 10% buffered formalin for 24 hours. The middle portions of eyed-side ovaries of 309 specimens were extracted, dehydrated, embedded in paraffin, sectioned at 8 μm, and stained with Mayer's hematoxylin and eosin (HE) and periodic acid Schiff (PAS).

Prepared sections were examined under a light microscope. The oocytes were then divided into eight stages according to the guidelines of Yamamoto (1956). Postovulatory follicles (POFs), which indicate spawning experience, were also examined. New POFs are easily identifiable, but those that have degenerated are difficult to distinguish from atretic follicles. In our study, only those that could be easily identified were defined as POFs. Atretic oocytes, namely advanced yolked oocytes that have been resorbed into the ovaries, were also determined; similarly, only those easily identifiable were defined as atretic oocytes. The percentage of advanced oocytes that were atretic was determined monthly for 10 randomly selected 2–7+ year-old fish (body size range: 143–210 mm SL).

Maturity was classified by the stage of the most advanced oocyte and the presence of POFs. By observing maturity and advanced oocyte diameter, we tested 15 ovaries for possible differences in oocyte development between anterior, middle, and posterior positions in the eyed-side ovary lobe, and between eyed-side and blind-side ovary lobes.

Oocyte diameter distributions in the late vitellogenic maturity phase were examined; the reason this maturity phase was selected is described in the "Results" section. The diameters of 50 randomly selected oocytes, extracted from the middle portions of the ovaries, were measured under a dissecting microscope to the nearest 20 μm. Potential fecundity was estimated with the gravimetric method by using ovaries in the late vitellogenic maturity phase. Extracted ovaries were rinsed and then weighed to the nearest 0.0001 g, and only developing oocytes, whose size is also described in the "Results" section, were counted.

Age was determined for all fish samples. Blind-side otoliths were used for the analyses according to the methods of Ishito (1964). The lateral surfaces of the otoliths were polished with 1500-grit sand paper until the transparent zones were visible. Ishito (1964) revealed that one transparent zone is formed at the edge of the otolith each winter and suggested that this may be regarded as an annual mark. However, the most interior ring appears when fish are aged 0+ (Ishito, 1964); therefore the number of transparent zones minus the 0-year-old zone was the formula used for aging, and the relationship between age and potential fecundity was analyzed.

Results

Annual changes in gonadosomatic index and body condition

The annual changes in gonadosomatic index (GSI) and body condition (BC) are shown in Figure 2. The GSI was

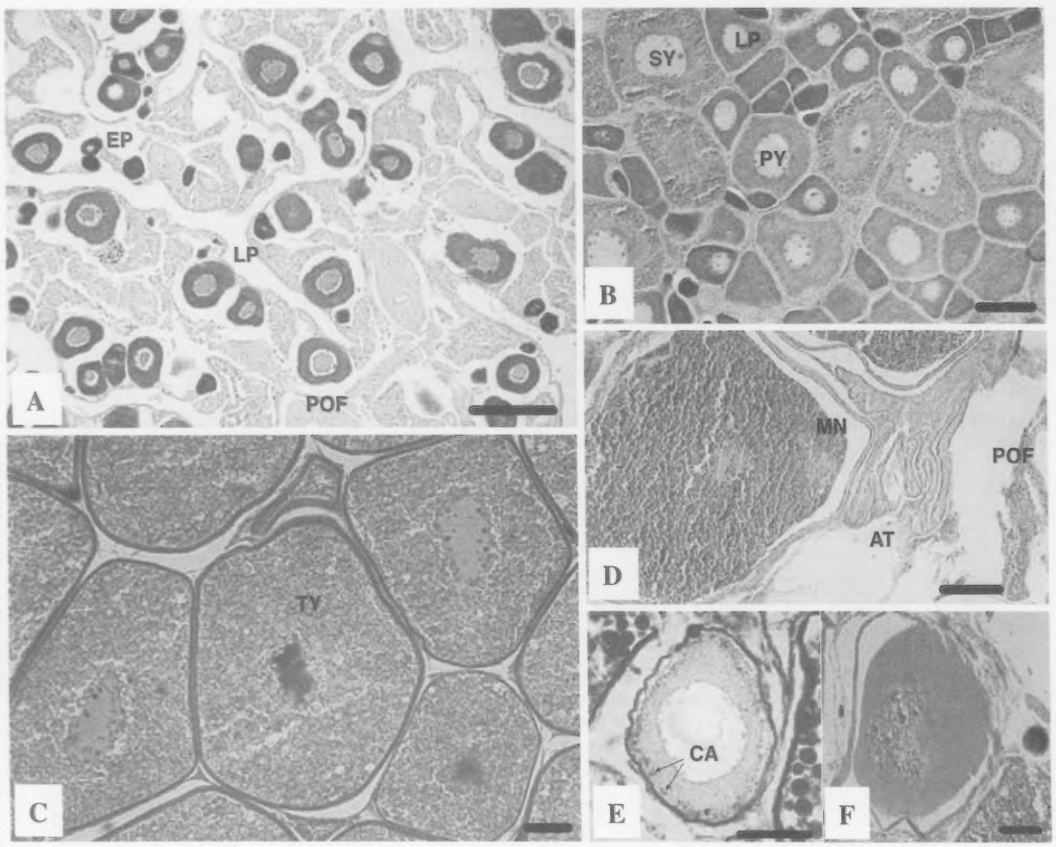

Figure 3

Histology of the ovarian maturity and oocyte developmental stages of Rikuzen sole (*Dexistes rikuzenius*). (**A**) Spent phase. Bar: 200 μm. (**B**) Middle vitellogenic phase. Bar: 200 μm. (**C**) Late vitellogenic phase. Bar: 200 μm. (**D**) Maturity phase. Bar: 200 μm. (**E**) Oocyte at the cortical alveolus stage. Bar: 50 μm. (**F**) Oocyte at the premature stage. Bar: 50 μm. EP=early perinucleolus stage, LP=late perinucleolus stage, CA=cortical alveolus, PY=primary yolk stage, SY=secondary yolk stage, TY=tertiary yolk stage, MN=migratory nucleus stage, AT=atretic oocyte, POF=postovulatory follicle.

relatively low, less than 2.0, from January to March, increased steeply from April to August, and progressed to more than 15.0 during September to October. Values then rapidly decreased from October to November. The BC was low from January to April, increased to a maximum value of 18.3 in August, and then decreased to 13.7 in November.

Histological observations of oocyte development

Although oogenesis is continuous, in order to explain the developmental process, oocyte development was divided into eight stages, basically according to Yamamoto (1956) (Fig. 3). The characteristics of oocytes, cell and nuclear diameters, and time of occurrence of each stage of oocyte and POF are shown in Table 1.

Maturity

Ovary maturity did not differ among positions in the ovarian lobe or between eyed-side and blind-side lobes. In addition, the diameters of the largest oocytes did not vary significantly among positions (ANOVA, $F_{2, 42}$= 0.354, P=0.704) or between lobes (paired t-test, f=14, t=0.058, P=0.955). Therefore, maturity was determined from observations of the middle portions of eyed-side ovaries.

Maturity was classified into eight phases, the characteristics of which are shown in Table 2. Because oocytes younger than the late perinucleolus stage occurred throughout the year, maturity was determined as occurring from this phase onwards. GSI values significantly varied among maturity phases (ANOVA, $F_{4,205}$,

Table 1

Characteristics, cell and nuclear diameters, and occurrence of oocytes and postovulatory follicles at each developmental stage. Developmental stage and measurements were determined by histological observations (EP=early perinucleolus, LP=late perinucleolus, CA=cortical alveoli, PY=primary yolk, SY=secondary yolk, TY=tertiary yolk, MN=migratory nucleus, PM=prematuration, POF=postovulatory follicle). HE=hematoxylin and eosin; PAS=periodic acid Schiff.

Developmental stage	Characteristics	Cell diameter (μm)	Nuclear diameter (μm)	Occurrence
EP	The ooplasm is strongly stained by haematoxylin. Several basophilic nucleoli stained by hematoxylin are present inside the nuclear membrane.	20–70	10–35	year round
LP	The ooplasm increases in volume with growth of the oocyte and becomes less basophilic than that of the previous EP stage.	70–150	35–80	year round
CA	Cortical alveoli, which appear in the ooplasm, are seen as a small empty spherical structure with conventional HE preparations, and are stained reddish by PAS reagents.	160–200	80–120	Feb, Jun, Aug, Oct
PY	The yolk granule occurs at the periphery of the oocytes.	180–220	80–120	year round
SY	The yolk granule increases in number and occurs towards the nuclear membrane, and the ooplasm occurs slightly at the periphery of the nuclear membrane.	260–440	90–130	Jan to Oct
TY	The oocyte is characterized by occupancy of the total volume of the oocyte by a yolk granule. The nucleus of the oocyte is still located at the center of the oocyte.	420–680	120–170	May to Dec
MN	The germinal vesicle migrates to the periphery of the oocyte and becomes elongated and globular in shape.	600–740	130–190	Sep to Dec
PM	The germinal vesicle has broken down. Yolk granules fuse with each other, and are stained light pink by eosin.	620–800	—	Sep to Nov
POF	The POF, containing granular, is a convoluted folded shape.	—	—	Sep to Jan

F=124.1, P<0.0001) and became significantly higher in each successive stage of maturity (Fisher's PLSD test, P<0.05), except for the first two phases (P=0.687). The mature- and spent-phase ovaries were excluded from the test because their values fluctuated depending on spawning times or the degree of POF absorption.

Ovaries in the late vitellogenic maturity phase, which occurred from May to September, contained oocytes in the tertiary yolk stage, secondary yolk stage, cortical alveoli stage, and late and early perinucleolus stages, but not in the primary yolk stage (Table 3). Ovaries in the premature phase, which occurred from September to October, also revealed two peaks and a hiatus in oocyte developmental composition. As described before, ovaries with POFs also contained maturing oocytes. These results show that this species is a multiple-spawner and has group-synchronous ovaries (Wallace and Selman, 1981; Takano, 1989); therefore, fecundity is fixed before spawning starts.

On the other hand, ovaries in the mid-vitellogenic phase were observed from January to September and contained oocytes in the secondary and primary yolk stages, and in the late perinucleolus stage. Cortical alveoli are very small and were present in only 10 of the 309 ovaries observed in our study. It is possible that the duration of this stage is very short. Therefore, in the ovaries oocytes do not divide into two groups, those that spawn in the next reproductive season and those that do not, until they have progressed to the late vitellogenic maturity phase.

Oocyte composition

Table 3 shows the annual changes in oocyte composition. One ovary observed in January contained POFs and perinucleolus stage oocytes, whereas the others contained oocytes in the primary and secondary yolk stages. Of those observed from February to April, none contained POFs. Frequency of occurence of ovaries with secondary yolk-stage oocytes increased during the season. From May to August the most advanced oocyte observed was in the tertiary-yolk vitellogenic stage, and the frequency of this stage also increased in number throughout this season. Migratory-nucleus–stage and

Table 2

The characteristics, occurrence and gondadosomatic index values of each maturity phase. Developmental oocyte stages were abbreviated as follows: EP=early perinucleolus, LP=late perinucleolus, CA=cortical alveoli, PY=primary yolk, SY=secondary yolk, TY=tertiary yolk, MN=migratory nucleus, PM=prematuration, POF=postovulatory follicle. n=number of samples. PAS=periodic acid Schiff.

Maturity phase	Characteristics	The most advanced oocyte observed	Occurrence	GSI (mean±SD)	n
Immature	Ovaries contain only EPs and LPs, but not POFs.	LP	Jan to Apr	1.57 ±0.34	13
Previtellogenic	This phase can be discriminated by PAS staining. Specimens in this phase were scarce.	CA	Feb	1.67	1
Early vitellogenic	Ovaries consist of PY and unyolked oocytes, and occur prevalently from March to April.	PY	Jan to Oct	2.09 ±0.61	41
Mid-vitellogenic	Ovaries contain SY and all stages of oocytes younger than the SY stage.	SY	Jan to Oct	4.40 ±1.72	61
Late vitellogenic	Ovaries contain TY and all stage oocytes younger than TY, but not SY.	TY	May to Dec	12.98 ±5.74	67
Premature	Ovaries lack PY and SY, occurs prevalently during September.	MN or PM	Sep to Dec	17.56 ±5.00	28
Mature	Ovaries contain both empty follicles and oocytes that have advanced beyond the secondary yolk stage.	advanced more than SY	Sep to Dec	16.21 ±8.34	25
Spent	Ovaries contain empty follicles but oocytes that have advanced beyond the secondary yolk stage are absent.	LP	Sep to Jan	2.71 ±2.41	73

premature-stage oocytes and POFs began to occur in September. The composition of oocytes observed during this month was divided into three groups: premature, maturing, and postmature oocytes. In October, almost all ovaries (96.2%) contained POFs. Of these, 28.0% also contained oocytes at the tertiary yolk stage or migratory-nuclear stage (or at both stages) and the remaining 72.0% contained primary-yolk stage or less advanced stage oocytes (or both of these stages). From November to December, all ovaries contained POFs and only a few (3.7% in November and 5.3% in December) also contained vitellogenic oocytes. Therefore, almost all individuals had finished spawning by October, although a few continued to spawn until December.

Atretic oocytes were found in samples throughout the year, except February, in ovaries of various maturity phases. Frequency of occurrence was highest in May, and gradually decreased until the spawning season (Table 3). Oocytes that ovulated but remained in the ovigenous folds and were resorbed later were treated as atretic oocytes because it was difficult to distinguish between them and atretic oocytes if they were somewhat absorbed. Atretic oocytes did not always correspond to the most advanced oocytes in the ovaries. They occupied 0.3–1.8% (mean ±SD=1.0 ±0.5) of the yolked, advanced oocytes observed in the ovaries in May (the number of oocytes counted in 10 ovaries ranged from 117 to 615), and from 0.4 to 1.8% (1.0 ±0.4) of those observed in August (range: 108–383 oocytes in 10 ovaries).

Body length and age at first maturity

The relationship between SL or age and maturity of the fish caught between the prespawning month (August) and the late-spawning month (December) was examined. Otolith growth increments were counted for all specimens. Because the spawning season occurs from September to December, the birth dates of all fish were conveniently defined as 1 January; age was then determined accordingly. SL ranged from 114 to 237 mm (n=189, 170.6 ±25.3) and age, from 1 to 8+ years (2.8 ±1.4). Individuals grew steeply until 2 years and moderately until 6 years, after which time their growth was slow (Fig. 4). All females whose ages were estimated at more than 2+ years (n=152) were identified as maturing or spent-stage females. Only one 1+ year-old specimen (131 mm SL) was classified as immature, whereas the other 1+ specimens (n=36, 140.0 ±11.8) were classified as maturing or postmaturation females (Fig. 4).

Potential fecundity

The diameters of oocytes in late vitellogenic maturity phase ovaries were measured because potential fecundity was determined as occurring before this maturity phase. Oocytes ranged in diameter from less than 100 to 950 μm and were separated into a small (less than 200 μm) or large group (larger than 300 μm, Fig. 5).

Table 3

Annual changes in the composition of female Rikuzen sole oocytes in each maturity phase. Some maturing and spent ovaries contained ovulated but not spawned oocytes. Such ovaries were included under "Number of samples with atretic oocytes." Developmental oocyte stages were abbreviated as follows: EP=early perinucleolus, LP=late perinucleolus, CA=cortical alveoli, PY=primary yolk, SY=secondary yolk, TY=tertiary yolk, MN=migratory nucleus, PM=prematuration, POF=postovulatory follicle.

Year	Month	EP	LP	CA	PY	SY	TY	MN	PM	POF	*n*	Maturity phase	Number of samples with atretic oocytes
2000	May	+	+		+						4	Early vitellogenic	4
		+	+		+	+					19	Mid vitellogenic	15
		+	+			+	+				1	Late vitellogenic	1
	Jun	+	+		+	+					18	Mid vitellogenic	10
		+	+	+	+	+					1	Mid vitellogenic	0
		+	+			+	+				3	Late vitellogenic	2
	Jul	+	+		+	+					7	Mid vitellogenic	2
		+	+			+	+				4	Late vitellogenic	1
	Aug	+	+		+						1	Early vitellogenic	0
		+	+	+	+	+					1	Mid vitellogenic	0
		+	+		+	+					4	Mid vitellogenic	1
		+	+			+	+				33	Late vitellogenic	9
		+	+				+				1	Late vitellogenic	0
	early Sep	+	+		+	+					2	Mid vitellogenic	1
		+	+			+	+				4	Late vitellogenic	0
		+	+				+				6	Late vitellogenic	2
		+	+	+			+	+			1	Premature	0
		+	+				+	+			8	Premature	1
		+	+				+	+	+		2	Premature	1
		+	+							+	4	Spent	1
		+	+	+						+	3	Spent	1
		+	+				+	+		+	11	Mature	3
		+	+				+	+	+	+	2	Mature	0
	late Sep	+	+			+	+				3	Late vitellogenic	0
		+	+	+			+				1	Late vitellogenic	0
		+	+				+				12	Late vitellogenic	2
		+	+	+			+	+			1	Premature	0
		+	+				+	+			12	Premature	1
		+	+				+	+	+		2	Premature	1
		+	+				+	+		+	3	Mature	2
	Oct	+	+				+	+			1	Premature	0
		+	+							+	10	Spent	4
		+	+	+						+	1	Spent	0
		+	+		+					+	7	Spent	4
		+	+				+			+	2	Mature	1
		+	+				+	+		+	5	Mature	3
	Nov	+	+							+	24	Spent	15
		+	+		+					+	2	Spent	1
		+	+				+	+		+	1	Mature	1
	Dec	+	+							+	13	Spent	5
		+	+		+					+	5	Spent	1
		+	+				+	+		+	1	Mature	0

continued

Those in the large-diameter group were regarded as advanced yolked oocytes that would be spawned in the next reproductive season and were used for estimations of potential fecundity. Potential fecundity varied widely among individuals from 24,765 (114 mm SL) to 393,212 (204 mm SL) eggs (an average of 161,340 ±90,688 eggs (165 ±25 mm SL)). Potential fecundity (PF) was positively correlated with body size and the relationship was expressed by the following equation:

$$PF = 0.000235SL^{3.96} \quad \text{(Fig. 6)}.$$

Potential fecundity and relative fecundity (potential fecundity/eviscerated body weight) increased with

Table 3 (continued)

Year	Month	EP	LP	CA	PY	SY	TY	MN	PM	POF	*n*	Maturity phase	Number of samples with atretic oocytes
2001	Jan	+	+								2	Immature	1
		+	+		+						8	Early vitellogenic	0
		+	+		+	+					2	Mid vitellogenic	0
		+	+							+	1	Spent	0
	Feb	+	+								5	Immature	0
		+	+	+							1	Previtellogenic	0
		+	+		+						5	Early vitellogenic	0
		+	+		+	+					1	Middle vitellogenic	0
	Mar	+	+								3	Immature	0
		+	+		+						15	Early vitellogenic	2
		+	+		+	+					1	Mid vitellogenic	1
	Apr	+	+								3	Immature	0
		+	+		+						10	Early vitellogenic	3
		+	+		+	+					6	Mid vitellogenic	1
	Total										309		104

growth at age ≤6+ years and decreased at ≥7+ years (Fig. 7). Comparisons of the relative fecundity among age groups (1–2+, 3–4+, 5–6+, and 7–8+) revealed significant differences with age (ANOVA, $F_{3,38}$=7.431, P<0.0005). In addition, *post hoc* tests (Fisher's PLSD, P<0.05) revealed significant differences between the following age groups: 1–2+ and 3–4+, 1–2+ and 5–6+, and 5–6+ and 7–8+. The GSI and BC values of individuals aged ≥7+ years were also lower than those of individuals aged 5+ and 6+ years, but the differences were not significant (*aq*-test, P>0.05); however, the sample size was very small; therefore the tests have little power.

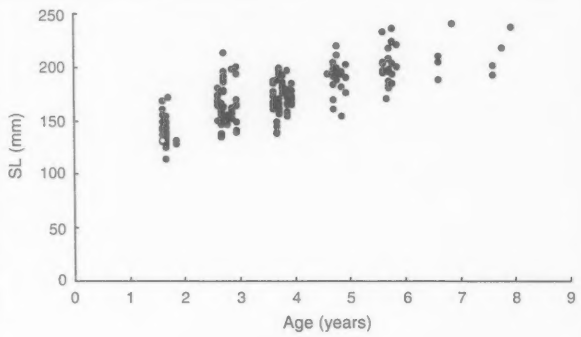

Figure 4

Relationship between age, including maturity, and the standard length of Rikuzen sole (*Dexistes rikuzenius*) caught between August and December. Solid circles represent maturing or spent individuals and the open circle at age 1+ represents an immature individual.

Discussion

Gonadal maturation

GSI and histological examinations showed that oocytes develop rapidly from May to August and that the reproductive season lasts from September to December; mainly from September to October in the study area. Mature females in the Sendai Bay area were also observed for four months, but the reproductive season in this area occurs from October to January and peaks in November (Ogasawara and Kawasaki, 1980), which was later than the peak documented in the present study for the area off the Hachinohe coast. The Sendai Bay catch area was located at a lower latitude (37°00′N–38°05′N; Ogasawara and Kawasaki, 1980) than that of the Hachinohe study area (Fig. 1); this difference is relevant because gonadal maturation is usually dependent on water temperature (Kruse and Tyler, 1983; Asahina and Hanyu, 1983; Conover, 1990). In 2000, the water temperature in the Hachinohe study area decreased faster than that of Sendai Bay in 1977 and 1978 when studied by Ogasawara and Kawasaki (TNFRI[1]). These results indicate that gonadal maturation in Rikuzen sole also depends on water temperature.

[1] TNFRI (Tohoku National Fisheries Research Institute). 2004. Unpubl. data. Water temperature data. Tohoku National Fisheries Research Institute, Fisheries Research Agency of Japan. Shiogama City, Miyagi Prefecture 985-0001 Japan.

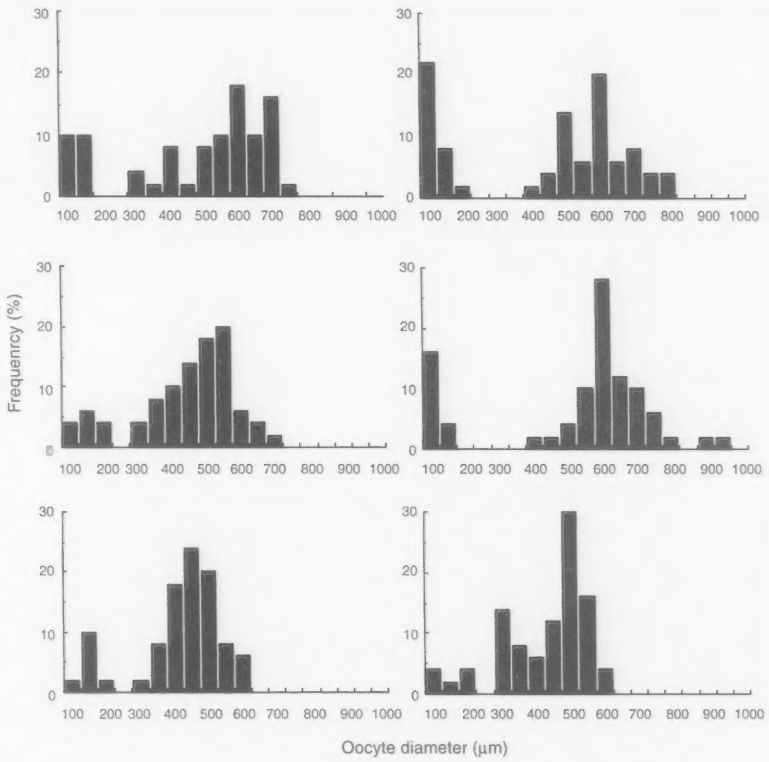

Figure 5

Oocyte diameter distributions just before the spawning season of Rikuzen sole (*Dexistes rikuzenius*). Oocyte diameter was divided into small-scale (less than 200 μm) and large-scale groups (more than 300 μm).

Rikuzen sole require a long period of time for vitellogenesis and therefore the reproductive cycle may differ among areas.

In some flatfishes, it has also been reported that oocytes in the cortical alveoli stage appear for only a short period of time because they develop rapidly into the primary yolk stage (Yamamoto, 1956; Janssen et al., 1995). In the present study, only a small percentage of individuals contained this stage of oocytes; however, cortical alveoli were present throughout various months from June to October and in February. These results are similar to results for other flatfish and may indicate that the absence of cortical alveoli oocytes in some ovaries does not represent an incontinuity of oocyte composition.

From October to December some females possessed primary yolk-stage oocytes,

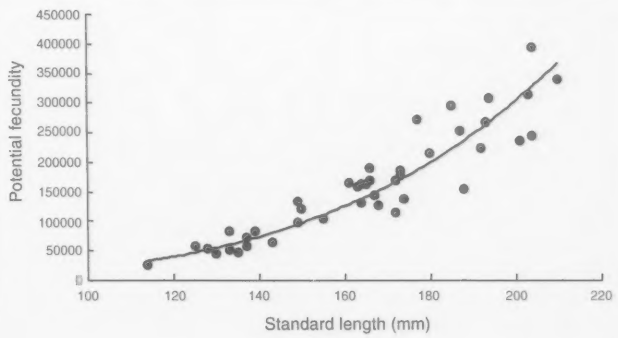

Figure 6

Relationship between the standard length and potential fecundity of Rikuzen sole (*Dexistes rikuzenius*). Potential fecundity was measured only for advanced yolk oocytes in late vitellogenic maturity phase ovaries. The equation of the regression curve is shown in the text.

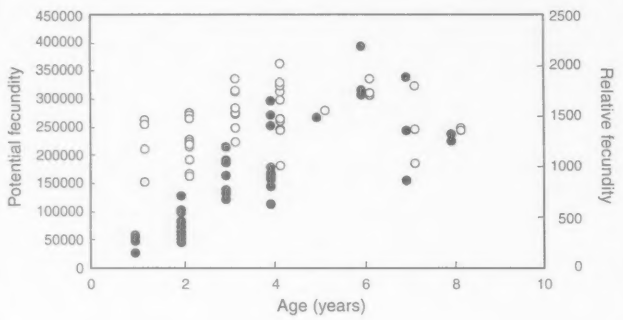

Figure 7

Relationship between age (years) and potential fecundity (solid circle, oocyte number/female) and relative fecundity (open circle, oocyte number/female per g) of Rikuzen sole (*Dexistes rikuzenius*) in the late vitellogenic maturity phase.

although they had no other vitellogenic oocytes. There are three potential hypotheses to explain the fate of these primary yolk oocytes. One explanation is that the oocytes are spawned in the current reproductive season. Maddock and Burton (1999) showed that in American plaice (*Hippoglossoides platessoides*), a group-synchronous spawner, the size frequency of oocytes during the prereproductive season was not continuous, whereas during the reproductive season the size frequency was continuous. The reason for this difference was that during the reproductive season cortical alveoli stage oocytes are larger than those during the prereproductive season. It is unclear, however, whether these cortical alveoli oocytes will be spawned during the reproductive season (Maddock and Burton, 1999). Although similar to those of the American plaice, all Rikuzen sole ovaries with primary yolk-stage oocytes contained no secondary or more advanced stage oocytes. In addition, oocytes that would be spawned in the current reproductive season developed beyond the secondary yolk stage before the beginning of the reproductive season. Therefore, primary yolk-stage oocytes occurring late in the reproductive season might not be spawned that season.

Primary yolk-stage oocytes were found from October to August (the late reproductive to vitellogenic season) (Table 3). From October to December only a small percentage of individuals possessed oocytes in this stage, whereas their ratio increased from January to April. These results indicate that females begin vitellogenesis for the next reproductive season shortly after spawning. This hypothesis is supported by reports that the vitellogenesis of flatfishes takes a long time (Yamamoto, 1954, 1956; Ishida and Kitakata, 1982; Zamarro, 1992; Harmin et al., 1995).

Atretic oocytes were present in low proportions from March to April and in high proportions in May. The mature phase of ovaries with atretic oocytes did not differ from that of ovaries without atretic oocytes. In addition, developmental stage did not differ between atretic and normal oocytes in any ovary. Therefore, it seems that the primary yolk-stage oocytes observed late in the reproductive season will not selectively degenerate, rather they will be spawned.

Decisions regarding maturity and age at maturity

POFs were present from September to January and all specimens caught during this period had either oocytes in the advanced yolk stage or POFs in their ovaries. All specimens caught between November and December contained ovaries with POFs, whereas they were observed only in a small percentage of the specimens caught in January. The spawning season lasted from September to December, but almost all spawning had finished by October. These results indicate that the duration until resorption of the POFs ranges from a few weeks to two months. For a few weeks immediately following spawning, the presence of POFs can be used as a criterion for the differences between post- and prespawning individuals. This feature is consistent with that of other flatfish in which POFs degenerate within one or two months (Barr, 1963; Janssen et al., 1995).

By noting the presence of POFs and advanced yolked oocytes, we were able to classify individuals as mature or immature. All but one individual caught during the reproductive period were maturing or had spawned. The body size of the mature females ranged from 114 to 237 mm SL, which corresponded to an age from 1 to 8+ years, respectively, whereas the immature female (131 mm SL) was age 1+. These results indicated that most female Rikuzen sole in this population mature at 2 years old, or at the latest at 3 years old, and spawn every year after maturation. Almost all (99.5%) fish caught commercially are adult individuals.

Fecundity

The potential fecundity of group-synchronous spawning fish can be determined prior to the spawning season (Takano, 1989). In Rikuzen sole, oocyte-stage composition became discontinuous beyond the late vitellogenic maturity phase, when a gap was found between secondary or tertiary yolk stages and the late perinucleolus stage. Oocyte diameter distributions in late vitellogenic maturity phase ovaries revealed that oocytes could be divided into small (less than 200 μm) and large (more than 300 μm) scale groups. Taking into account the oocyte diameters observed in the histological sections, small-scale group oocytes corresponded to cortical alveoli or less advanced stage oocytes, whereas larger oocytes corresponded to secondary yolk or more advanced stage oocytes.

The occurrence of atretic oocytes was highest in May and became lower as the season progressed until the end of the spawning season. These phenomena may correlate with both annual feeding cycles and maturation. Ogasawara and Kawasaki (1980) showed that in the Sendai Bay population, Rikuzen sole feed actively for a few months after spawning and then feed passively for the next few months. Gut-content weight began to increase again in June. In our study area, BC increased from about May, corresponding to the time when the oocytes begin to mature rapidly. As described before, vitellogenesis in this species takes a long time. Because oocytes are metabolically active in the season when the energetic condition of Rizuzen sole is still recovering, a higher proportion of atretic oocytes occur during this period.

Potential fecundity may not correspond to annual fecundity because of the presence of atretic and residual oocytes (Witthames and Greer Walker, 1995; Kurita et al., 2003). Therefore, we examined the potential fecundity of fish in the late vitellogenic maturity phase just before the spawning season. The frequency of occurrence of atretic oocytes may be underestimated because these oocytes have shrunk and are smaller than the maturing yolked oocytes. In addition, atretic oocytes may occur in the ovaries during the premature maturity phase. However, in our samples a low percentage of atretic oocytes were observed. Only a small percentage of premature ovaries were found on or before the reproductive season; this finding seems to indicate that the oocytes of this species take a short time to develop from the tertiary vitellogenic stage to maturation. These results make clear that potential fecundity differs from annual fecundity, but the extent of this difference was nevertheless relatively small in the samples. Moreover, ovulated, but not spawned oocytes were observed in the maturing and spent ovaries; these oocytes have the potential to cause an overestimation of annual fecundity. However, the frequency of ovaries with residual ovulated oocytes was small; therefore, such oocytes may not seriously influence annual fecundity, as with the case of Dover sole (*Microstomus pacificus*) (Hunter et al., 1992).

Vitellogenesis in American plaice was seen to begin soon after spawning (Zamarro, 1992), as with Rikuzen sole. Separation of oocyte diameter in this species occurs approximately three months before the start of the spawning season. In Rikuzen sole, potential fecundity was determined as being much closer to the reproductive season. Reproduction occurred from early September, but occurrence of the maturity phase in August varied largely among individuals. The potential fecundity of almost all fish (85%) could be determined until August. These results indicate that certain conditions and measurements are necessary when examining potential fecundity without histological methods.

Potential fecundity became determinate for the first time at maturity during the late vitellogenic phase. Some of the maturity phase ovaries contained secondary yolk-stage oocytes and all contained tertiary yolk-stage oocytes. The secondary yolk-stage oocytes ranged in diameter from 260 to 440 μm—a range that does not overlap with the diameter range of primary yolk-stage oocytes (180–220 μm). Therefore, to measure potential fecundity without histological observations, it is first necessary to clarify the division of oocyte diameter into large- and small-scale groups in order to identify determinate fecundity. In ovaries that contain large- and small-scale oocytes, only oocytes greater than 260 μm in diameter but that do not experience ovulation between May and August are targets for potential fecundity measurements. This method will make it easier to measure the potential fecundity of this population in the future.

Potential fecundity increased curvilinearly with SL. The body size of the females continued to grow even after maturation; the most fecund individual had 15 times more maturing oocytes than the least fecund one. Potential fecundity also increased until age ≤6+ years but decreased in individuals at ≥7+ years. One reason that older fish have less potential fecundity is a lesser energetic condition with senescence. Fecundity has been also reported as declining with age in other fish. As American plaice in the tail of the Grand Bank of Newfoundland become older, the number of eggs produced by females decreased (Horwood et al., 1986). Orange roughy, mature first at 25 years old and live for more than 100 years; their fecundity increases from an age of 25 to 60 years old, then decreases in individuals aged over 60 years old (Koslow et al., 1995). Fecundity is positively correlated with BC in the orange roughy. The oldest Rikuzen sole to appear in that study area was 10+ years (Ishito, 1964) and body growth almost finished by age 6+ years (Fig. 6). In addition, both the BC and relative fecundity of fish over 7+ years were lower than those of fish from 4 to 6+ years.

Spawning stock biomass (SSB) has been used to examine the relationship of spawning fish and recruitment; however, recent studies have indicated that SSB is not always linked to reproductive potential, mainly because age composition and nutrient conditions also affect fecundity (Hunter et al., 1985a; Trippel et al., 1997; Marshall et al., 1998). Our study shows that relative fecundity is positively correlated with body length. In addition, both relative and potential fecundity increase

with age, but decrease again in later years. These results support previous studies and emphasize the importance of understanding the demographic structure and reproductive biology of a population for the management of fish resources.

Acknowledgments

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Temporal and spatial distribution and abundance of flathead sole (*Hippoglossoides elassodon*) eggs and larvae in the western Gulf of Alaska

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Abstract—Data from ichthyoplankton surveys conducted in 1972 and from 1977 to 1999 (no data were collected in 1980) by the Alaska Fisheries Science Center (NOAA, NMFS) in the western Gulf of Alaska were used to examine the timing of spawning, geographic distribution and abundance, and the vertical distribution of eggs and larvae of flathead sole (*Hippoglossoides elassodon*). In the western Gulf of Alaska, flathead sole spawning began in early April and peaked from early to mid-May on the continental shelf. It progressed in a southwesterly direction along the Alaska Peninsula where three main areas of flathead sole spawning were indentified: near the Kenai Peninsula, in Shelikof Strait, and between the Shumagin Islands and Unimak Island. Flathead sole eggs are pelagic, and their depth distribution may be a function of their developmental stage. Data from MOCNESS tows indicated that eggs sink near time of hatching and the larvae rise to the surface to feed. The geographic distribution of larvae followed a pattern similar to the distribution of eggs, only it shifted about one month later. Larval abundance peaked from early to mid-June in the southern portion of Shelikof Strait. Biological and environmental factors may help to retain flathead sole larvae on the continental shelf near their juvenile nursery areas.

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Fish. Bull. 103:648–658 (2005).

Flathead sole (*Hippoglossoides elassodon*) inhabit the continental shelf waters of the North Pacific Ocean from the northwest coast of North America to the Sea of Okhotsk in Asia (Alderdice and Forrester, 1974). The western Gulf of Alaska is an important area for adult, juvenile, and larval flathead sole. The continental shelf from the entrance to Prince William Sound to Unimak Island contains the highest relative abundance of adult flathead sole (as expressed as kg/ha) off the west coast of North America (Fig. 1; Wolotira et al.[1]). Adult flathead sole are most abundant between depths of 100 and 200 m in this area (Wolotira et al.[1]). During the spring adult flathead sole move from wintering grounds on the upper continental slope onto the continental shelf (Rose, 1982). Spawning flathead sole are found from February to August, and the greatest proportion of spawning fish occurs in April and May at depths between 100 and 200 m (Hirschberger and Smith[2]). Flathead sole eggs range in size from 2.75 to 3.75 mm (Matarese et al., 1989), and under environmental conditions similar to those they could experience in the Gulf of Alaska (temperature=5.5°C and salinity=31 PSU) it takes them about 15 days to hatch (Alderdice and Forrester, 1974). During the spring, flathead sole are the most abundant pleuronectid larvae in western Gulf of Alaska (Rugen[3]). Standard length at hatching is 6.89 ±0.40 mm (95% ethanol-preserved size; S. Porter unpubl. data). Under conditions that flathead sole larvae could experience in the Gulf of Alaska, first feeding occurs about 1 week after hatching, and in about 2 weeks the yolk is exhausted (Alderdice and Forrester, 1974). Copepod nauplii 150–350 μm in size are their predominant prey (Watts, 1988). In Auke Bay, Alaska, flathead sole larvae undertake reverse diel vertical migrations; they are concentrated near 5 m depth during the day and then disperse over a wider range of depths at night (Haldorson et al., 1993). The bays of the Alaska Peninsula and Kodiak Island provide nursery areas for juvenile flathead sole (Norcross et al., 1999).

Studies of the drift of walleye pollock (*Theragra chalcogramma*) larvae in Shelikof Strait have shown that there are physical processes that can slow the drift of these larvae out of Shelikof Strait and keep them near shore (Bailey et al., 1997). The pro-

[1] Wolotira, R. J., T. M. Sample, S. F. Noel, and C. R. Iten. 1993. Geographic and bathymetric distributions for many commercially important fishes and shellfishes off the west coast of North America, based on research survey and commercial catch data, 1912–84. NOAA Tech. Memo. NMFS-AFSC-6, 184 p. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

[2] Hirschberger, W. A., and G. B. Smith. 1983. Spawning of twelve groundfish species in the Alaska and Pacific coast regions, 1975–81. NOAA Tech. Memo. NMFS F/NWC-44, 50 p. Northwest and Alaska Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98112.

[3] Rugen, W. C. 1990. Spatial and temporal distribution of larval fish in the western Gulf of Alaska, with emphasis on the period of peak abundance of walleye pollock (*Theragra chalcogramma*) larvae. U.S. Dep. Commer., NWAFC Processed Rep. 90-01, 162 p. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

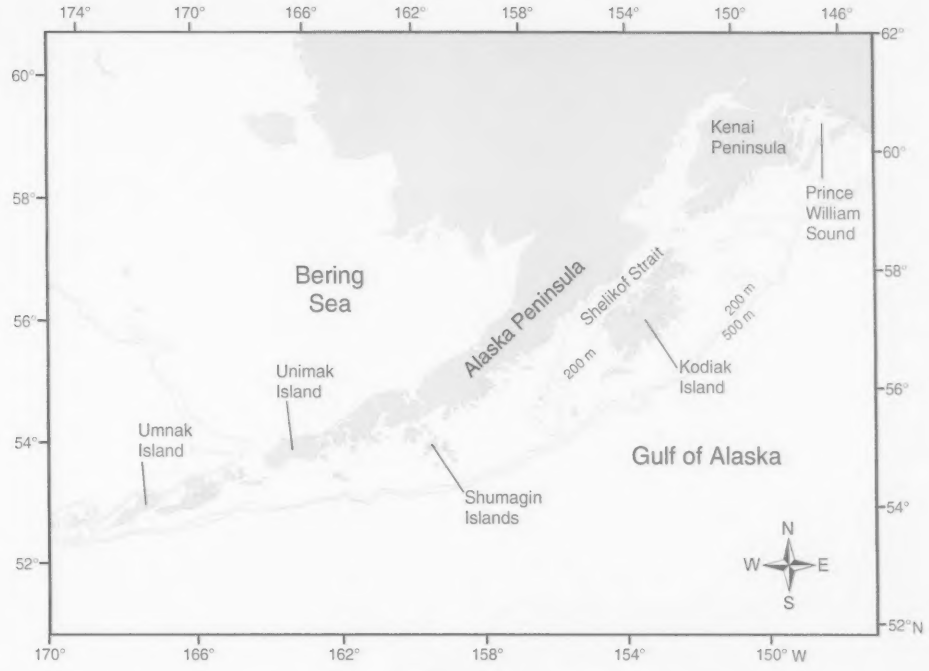


Figure 1

The western Gulf of Alaska where ichthyoplankton surveys were conducted in 1972 and from 1977 to 1999 by the Alaska Fisheries Science Center to examine the timing of spawning, geographic distribution and abundance, and vertical distribution of flathead sole (*Hippoglossoides elassodon*).

cesses that affect the drift of walleye pollock larvae may also affect the drift of flathead sole larvae in this area. For example, the drift of walleye pollock larvae in Shelikof Strait can be slowed if they become entrained in eddies that form there (Bailey et al., 1997). The Alaska Coastal Current flows southwest through Shelikof Strait and branches just south of it; one branch continues along the continental shelf, and the other heads seaward (Bailey et al., 1997). Whether larvae will stay near shore or move off shore is determined by one or other of these two branches of the current.

Information about the early life history of flathead sole in the Gulf of Alaska is lacking. Data from ichthyoplankton surveys conducted in the western Gulf of Alaska were used to examine the timing of spawning, geographic distribution and abundance, and the vertical distribution of flathead sole eggs and larvae. The purpose of this study was to give a general overview of flathead sole egg and larval distribution and abundance in the Gulf of Alaska during the calendar year.

Materials and methods

The study area covered the continental shelf (approximately 300 m depth and less) of the western Gulf of Alaska from the Kenai Peninsula southwest along the Alaska Peninsula to Umnak Island (Fig. 1). Also covered was the east side of Kodiak Island out to the continental shelf break (Fig. 1). The Alaska Stream and the Alaska Coastal Current are two major surface currents that flow through the study area. Both currents flow southwesterly: the Alaska Stream along the shelf break and the Alaska Coastal Current through Shelikof Strait (Kendall et al., 1996).

A series of ichthyoplankton surveys were conducted in 1972 and from 1977 to 1999 (no data were collected in 1980) by the Alaska Fisheries Science Center (NOAA, NMFS) in the western Gulf of Alaska (Tables 1 and 2). Data were used from 75 surveys. Surveys were conducted from February to November; the most intensive sampling was in April and May. Not all months were sampled every year, and not all cruises surveyed the same area. A 60-cm diameter bongo sampler with a net mesh size of 333 or 505 μm was towed in a double oblique fashion (from the surface to near bottom and back to the surface) to collect samples used to examine the geographic distribution and abundance of eggs and larvae. Interannual variability in the abundance of eggs and larvae in the Shelikof Strait spawning area can vary as much as tenfold (S. Porter, unpubl. data), but to increase sampling coverage of the study area,

Table 1

The number of stations used each year to assess monthly flathead sole (*Hippoglossoides elassodon*) egg distribution in the western Gulf of Alaska.

Cruise year	Feb	Mar	Apr 1–15	Apr 16–30	May 1–15	May 16–31	Jun 1–15	Jun 16–30	Jul	Aug	Sep	Oct	Nov
1972	—[1]	—	—	27	40	—	—	—	—	—	—	—	—
1977	—	—	—	—	—	—	—	—	—	—	—	11	48
1978	—	23	61	2	—	—	—	69	20	—	57	67	118
1979	48	40	—	—	—	58	—	—	—	—	18	—	—
1981	—	190	61	123	16	136	—	—	—	—	—	—	—
1982	—	—	55	28	—	62	—	—	—	—	—	—	—
1983	—	—	—	—	1	67	—	—	—	—	—	—	—
1984	—	2	63	66	28	—	—	—	—	—	—	—	—
1985	—	109	87	28	62	135	54	—	—	—	—	—	—
1986	—	11	185	34	89	19	—	—	—	—	—	—	—
1987	—	—	177	83	—	59	—	15	4	—	—	—	—
1988	—	102	228	64	13	4	1	—	—	—	—	—	—
1989	—	—	128	69	132	47	1	—	—	—	—	—	—
1990	—	—	107	—	88	70	78	—	—	—	6	—	—
1991	—	—	90	150	119	97	—	—	—	—	—	—	—
1992	—	—	94	—	158	136	—	—	—	—	—	—	—
1993	—	—	96	—	141	90	24	—	—	—	—	—	—
1994	—	10	9	—	88	133	6	—	—	—	—	—	—
1995	1	5	—	—	—	98	—	—	—	—	—	—	—
1996	—	—	—	59	269	130	—	—	—	—	—	—	—
1997	—	—	—	—	—	100	—	—	—	—	—	—	—
1998	—	—	—	—	72	128	—	26	—	—	—	—	—
1999	—	—		—	2	233	83	—	—	—	—	—	—
Total	49	492	1436	733	1320	1803	247	110	24	0	81	78	166

[1] No stations.

years were pooled for each month. Abundance did not appear to affect the spatial distribution of eggs or larvae; their distribution patterns were similar no matter whether abundance was high or low. Months of highest abundance (April, May, and June) were divided into early to mid-month (days 1–15) and mid- to late month (days 16–31). The area covered by the cruises was divided into 50×50 km grid cells. Mean catch per cell was calculated for each grid cell, averaging over all stations falling within the cell. For the areas other than Shelikof Strait, the number of stations per cell ranged from 1 to 10. The most intensive sampling was conducted in the Shelikof Strait area, south to approximately 56°N latitude. Cells in this area, depending on the month, could have more than 100 stations within them. To examine larval drift, the center and ellipse (centroid) of egg and larval abundance for early and late May 1994 and 1996 (two years with different flow regimes in Shelikof Strait) were calculated according to the methods described in Kendall and Picquelle (1989).

The vertical distribution of eggs and larvae was examined from samples from four 1-m^2 MOCNESS (multiple-opening-closing-net and environmental sensing system) tows. For each tow, 6 to 8 depth intervals were sampled from near the sea floor to near the surface. The samples were collected during peak spawning in 1991 (one tow during day light), 1993 (one tow during day light), and 1996 (two tows: 1996A conducted during the night, and 1996B during day light). Eggs collected in each depth interval were categorized as early (stages 1–12), middle (stages 13–15), and late stage (stages 16–21) according to walleye pollock egg stages adapted from Blood et al. (1994). The late stage was divided into two categories: late A (stages 16–19) and late stage B (stages 20–21), to indicate which eggs were closest to time of hatching. Taking into account shrinkage in standard length due to collection and preservation (Theilacker and Porter, 1995), larvae were divided into three size categories based on development. Larvae <5 mm were classified as recently hatched, larvae 5–6 mm as prefeeding or first feeding, and larvae >6 mm as feeding, based not only on size but also on the amount of yolk present, and whether prey were visible in their gut. These categories were based on observations of flathead sole larvae

Table 2

The number of stations used each year to assess monthly flathead sole (*Hippoglossoides elassodon*) larval distribution in the western Gulf of Alaska.

Cruise year	Apr 1–15	Apr 16–30	May 1–15	May 16–31	Jun 1–15	Jun 16–30	Jul	Aug	Sep	Oct	Nov
1972	—[1]	27	40	—	—	—	—	—	—	—	—
1977	—	—	—	—	—	—	—	—	—	11	48
1978	60	2	—	—	—	69	20	—	57	67	118
1979	—	—	—	58	—	—	—	—	18	—	—
1981	61	123	16	136	—	—	—	—	—	—	—
1982	55	28	—	62	—	—	—	—	—	—	—
1983	—	—	1	63	—	—	—	—	—	—	—
1984	63	66	28	—	—	—	—	—	—	—	—
1985	87	28	62	135	54	—	—	—	—	—	—
1986	185	34	89	19	—	—	—	—	—	—	—
1987	177	83	—	58	—	15	4	—	—	—	—
1988	227	64	13	2	1	—	—	—	—	—	—
1989	128	69	132	34	1	—	—	—	—	—	—
1990	107	—	90	70	78	—	—	—	6	—	—
1991	90	150	119	97	—	—	—	—	—	—	—
1992	94	—	158	136	—	—	—	—	—	—	—
1993	96	—	141	90	24	—	—	—	—	—	—
1994	4	—	89	133	6	—	—	—	—	—	—
1995	—	—	—	98	—	—	—	—	—	—	—
1996	—	59	273	130	—	—	—	—	—	—	—
1997	—	—	—	100	—	—	—	—	—	—	—
1998	—	—	72	128	—	26	—	—	—	—	—
1999	—	—	6	233	83	—	—	—	—	—	—
Total	1434	733	1329	1782	247	110	24	0	81	78	166

[1] No stations.

reared in the laboratory (S. Porter, unpubl. data). In the laboratory, flathead sole larvae hatch with pigmented eyes, three tail pigment bands, and an open mouth (S. Porter, unpubl. data). Flathead sole larvae that were collected from MOCNESS tows and that did not have these features were classified as embryos (it was suspected that handling during collection may have caused some of the late stage eggs to prematurely hatch), and their lengths were not included in the weighted mean depth. For eggs and larvae, a weighted mean depth was calculated for each stage or size category, and depths were compared by using ANOVA and the Tukey HSD multiple comparison test.

Results

Eggs

Geographic distribution and abundance Eggs were collected as early as March but in small numbers (Figs. 2 and 3A). Most spawning began from early to mid-April (Fig. 3B) near the Kenai Peninsula and then progressed with time southwest into Shelikof Strait and along the Alaska Peninsula. There are two main areas where peak spawning (from early to mid-May) occurred: Shelikof Strait and between the Shumagin Islands and Unimak Island (Fig. 3C). In June, spawning generally declined in these areas and was most intense around Kodiak Island (3D). Eggs were collected as late as July (one station in 1978, on the eastern side of Kodiak Island).

Vertical distribution There were similar trends in the vertical distribution of eggs among tows (Fig. 4). Abundance peaked at about 20 to 35 m below the surface, decreased at greater depth, and then slightly increased below 125 m. Because the trend of the catches of the tows were similar, we were able to increase sample size in the depth intervals by pooling data from similar depth intervals for further analyses. Eggs were pelagic and most abundant near the surface (mean depth 43 ±10 m) and at the deep sampling depths (mean depth 149 ±6 m); abundance was low in mid-water (Fig. 4). Late-stage eggs (stages 16–21) dominated the depths of

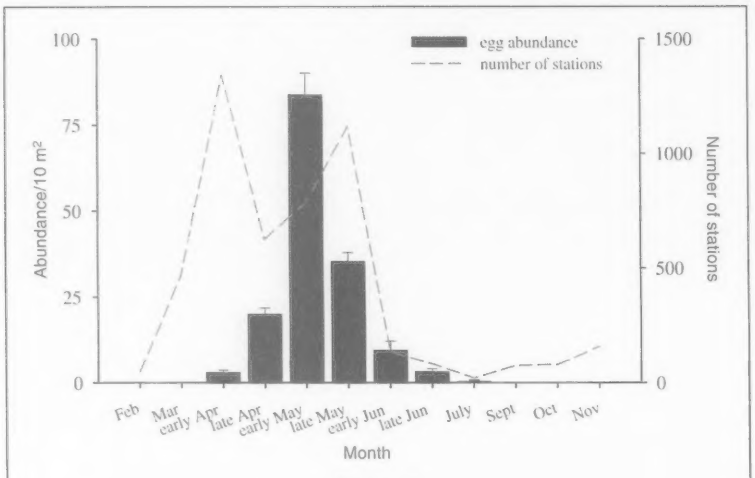


Figure 2

The mean abundance of flathead sole (*Hippoglossoides elassodon*) eggs in the western Gulf of Alaska during the year. Standard deviation and number of stations used for each time period are also shown. The abundance in March was very low (0.01 eggs/10 m^2).

high abundance. Early stage eggs were most abundant in mid-water; they accounted for 79% of the total number of eggs collected between 50 and 159 m depth. Sixty-six percent of all eggs collected above 66 m depth were middle- and late-stage A eggs. The largest numbers of late-stage B eggs were found below 124 m depth, where they accounted for 83% of all eggs collected. Mean egg stage depth showed that as the eggs developed from the early stages to the middle stages they rose toward the surface (mean depth of the eggs changed from 54 to 28 m); then in the later stages of development the eggs sank and hatched at depth. Late-stage B eggs were collected significantly deeper (mean depth 90 ±37 m) than late-stage A eggs (mean depth 35 ±7 m; ANOVA, P=0.007; Tukey HSD multiple comparison test, P=0.006).

Larvae

Geographic distribution and abundance Larvae were found from early April to October, but they were most abundant from mid-May to mid-June (Fig. 5). From mid- to late April, larvae were most abundant near the Kenai Peninsula (Fig. 6A), and as spring progressed their abundance increased southwest along the Alaska Peninsula (Fig. 6B). Peak abundance occurred during the first two weeks of June in the southern portion of Shelikof Strait (Fig. 6C). From mid- to late June larvae were most abundant on the east side of Kodiak Island (Fig. 6D). Although most of the surveys were conducted in this area, it is possible that larvae may have been abundant elsewhere in the study area during this time. From July through October, only the area east of Kodiak Island was surveyed, and larval abundance there was low.

Larval drift Satellite-tracked drifters released in May 1994 and drogued at 40 m indicated that the Alaska Coastal Current flow was strong and moving to the southwest—typical surface current flow for this area (Bailey[4]). In May 1996, drifters showed that flow was weak, disorganized and moving somewhat to the northeast (Bailey et al., 1999). In early May 1994, very few flathead sole larvae were collected; therefore the center point of the flathead sole egg distribution was used to infer the starting location of larval drift. Size-at-age data have shown that the growth rate for flathead sole larvae is 0.3 mm/day in Auke Bay, Alaska (Haldorson et al., 1989). Using this growth rate, we determined that larvae hatched in early May could have grown as much as 6 mm in the 21 days between surveys. The size class of larvae greater than 9 mm was assumed to include larvae that had hatched from the eggs present in early May. The location of the centers of distribution of the early May eggs and late May larvae indicated that the larvae had drifted southward over the continental shelf (Fig. 7). In 1996 all the larvae collected in early May were 7.1 mm and smaller (range 4.2 to 7.1 mm). The area was surveyed 26 days later, and growth of about 8 mm could have occurred between surveys. For larvae collected at the end of May, the size group longer than 12 mm was assumed to include the early May larval group. The location of the centers of distribution of the early May and late May larvae showed that the larvae were retained at nearly the same location (Fig. 8).

[4] Bailey, K. M. 2002. Personal commun. NOAA, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115.

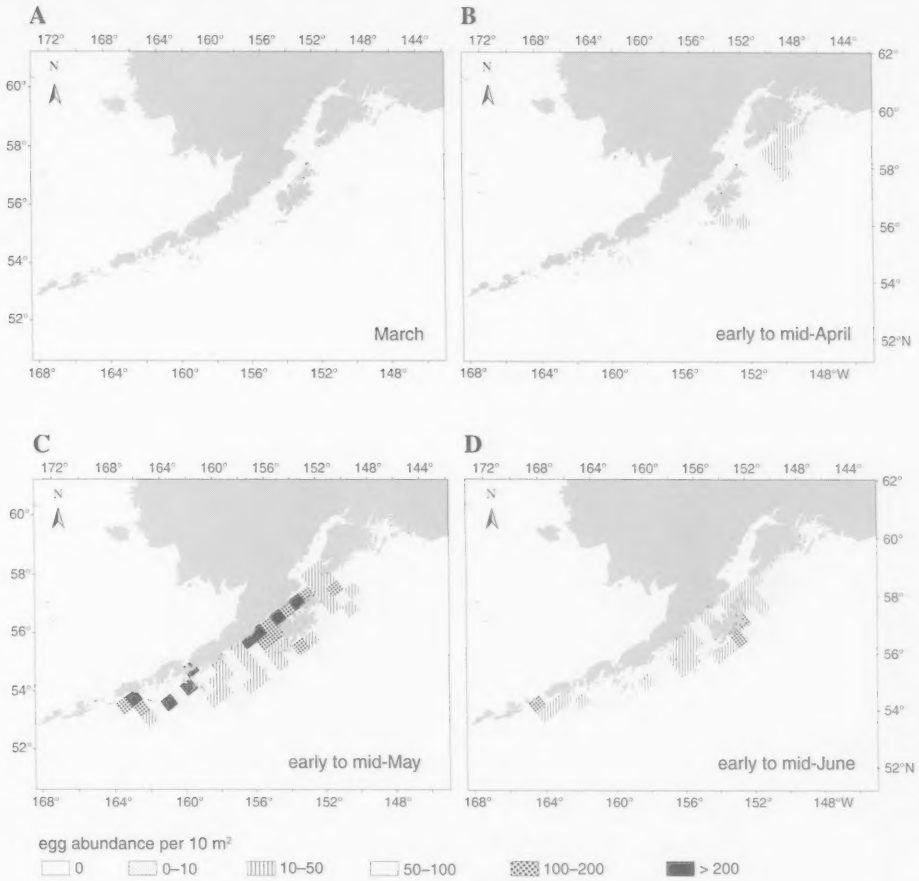


Figure 3

The geographic distribution of flathead sole (*H. elassodon*) eggs in the western Gulf of Alaska during the spawning season; (**A**) March, (**B**) early to mid-April, (**C**) early to mid-May, (**D**) early to mid-June.

Vertical distribution There were similar trends in the vertical distribution of larvae among tows (Fig. 9). Abundance peaked at about 15 to 30 m below the surface, then decreased, and larvae were collected from the deepest sampling depth interval from one tow (1996A; Fig. 9). Because the tows were alike, to increase sample size in the depth intervals, we pooled data from similar depth intervals but from different tows for further analyses. Larval abundance was highest near the surface and at the deepest depths sampled (Fig. 9). In Auke Bay, Alaska, flathead sole larvae migrated vertically at night no more than 15 m, ending at 20 m depth, and they were less aggregated (Haldorson et al., 1993). This depth was much shallower than the depth at which larvae and late-stage eggs were collected in tow 1996A (sampling depth interval was 174–236 m). Therefore the deep concentration of larvae in 1996 was probably due to eggs hatching rather than to vertical migration. The deepest sample comprised embryos and larvae (the larvae, however, were too damaged to determine whether they were prefeeding or feeding larvae), and samples collected above 100 m were a mixture of embryos and prefeeding larvae (29%), and feeding larvae (71%). The smallest larvae (<5 mm) were found in deepest water (mean depth 166 ±32 m), and larger larvae (≥5 mm) were found in shallower water (above about 60 m depth; ANOVA, $P<0.001$; Tukey HSD multiple comparison test, $P<0.001$). The size distribution of the larvae indicated that soon after hatching they rise to the surface to feed.

Discussion

Flathead sole inhabit the continental shelf of the North Pacific Ocean, and the area used for the present study

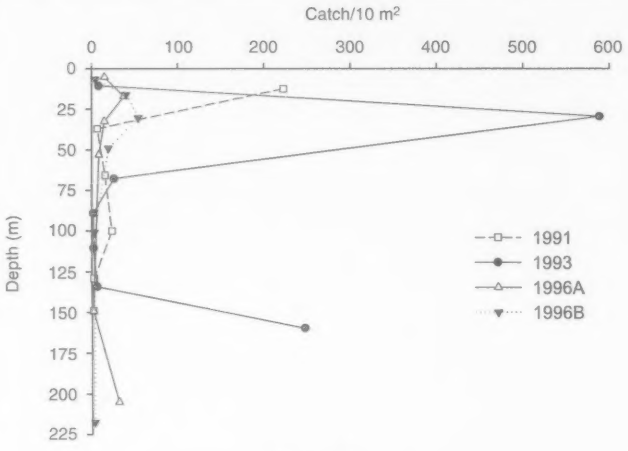


Figure 4

The vertical distribution of flathead sole (*H. elassodon*) eggs collected from four MOCNESS tows conducted in 1991, 1993, 1996 during peak spawning. Symbols indicate the mean of the depth interval that the samples were collected in.

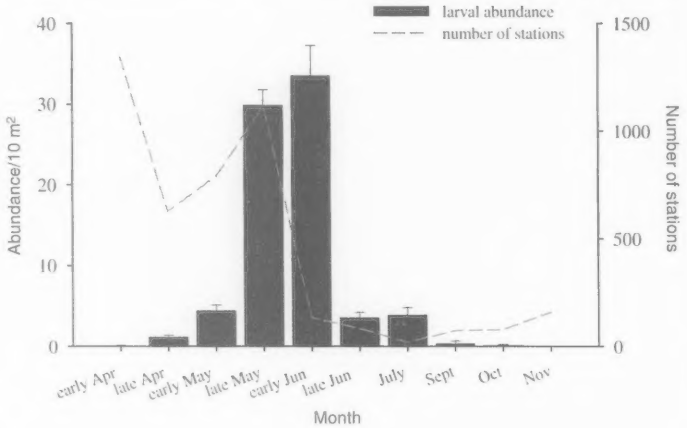


Figure 5

The mean abundance of flathead sole (*H. elassodon*) larvae in the western Gulf of Alaska during the year. Standard deviation and number of stations used for each time period are also shown. Abundance in early April and October was very low, 0.06 and 0.11 larvae/10 m², respectively.

contains the highest relative abundance of adult flathead sole off the west coast of North America (Wolotira et al.[1]). Generally, outside the study area the abundance of adult flathead sole is low (Wolotira et al.[1]); therefore these areas most likely had very little effect on the abundance of eggs and larvae collected from within the study area.

In the western Gulf of Alaska flathead sole spawn in three main areas during the spring: near the Kenai Peninsula, in Shelikof Strait, and in the area between the Shumagin Islands and Unimak Island. Spawning progresses in a southwesterly direction along the Alaska Peninsula. Flathead sole in spawning condition are abundant from March through May (Hirschberger and

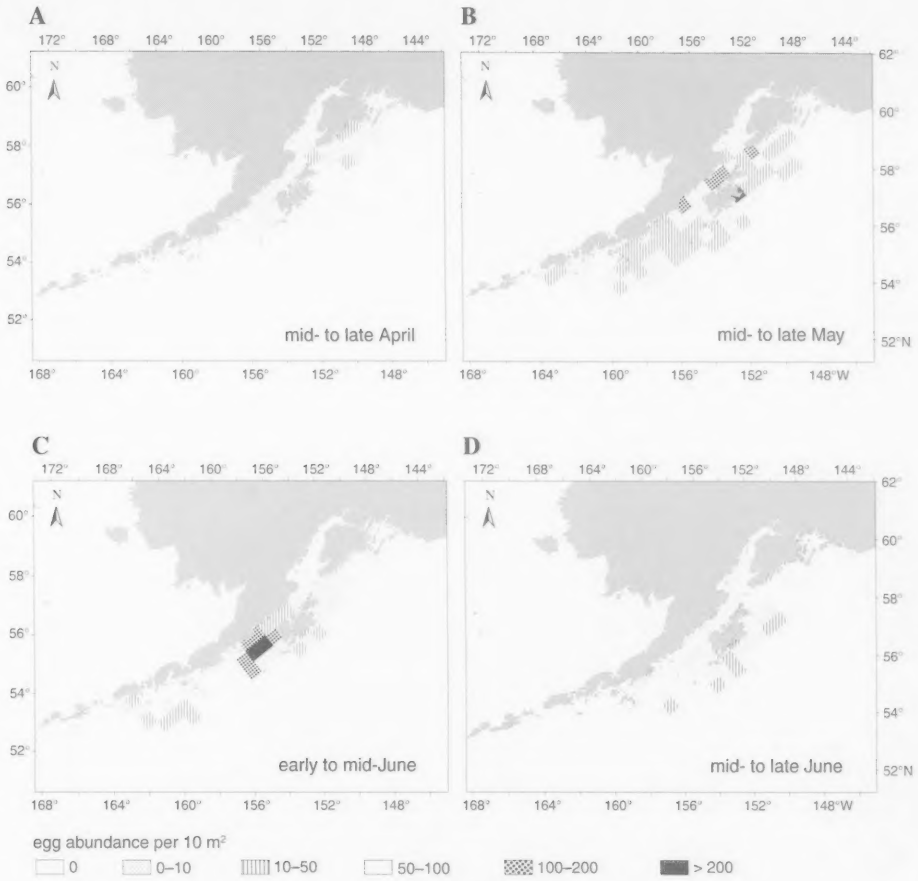
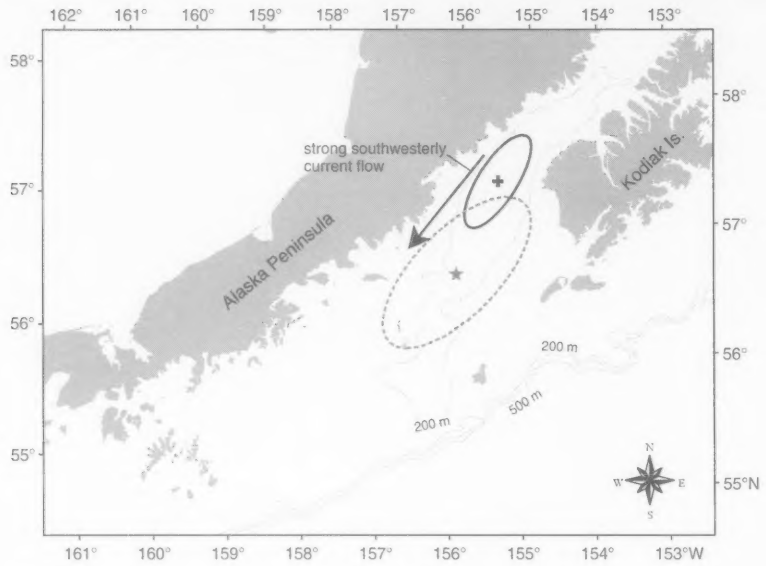


Figure 6

The geographic distribution of flathead sole (*H. elassodon*) larvae in the western Gulf of Alaska during months of the spawning season. (**A**) mid- to late April, (**B**) mid- to late May, (**C**) early to mid-June, (**D**) mid- to late June.

Smith[2]), which correlates with the period when eggs were collected in the present study. Peak spawning occurred from early to mid-May, and by the end of June spawning was nearing completion. Larval abundance peaked from early to mid-June in the southern portion of Shelikof Strait. In late July, late-stage flathead sole larvae were the most abundant of larval fish collected in the Gulf of Alaska between the Semidi Islands and Unimak Island (Brodeur et al., 1995). Flathead sole larvae have also been found on the east side of Kodiak Island during the summer (Kendall and Dunn, 1985).

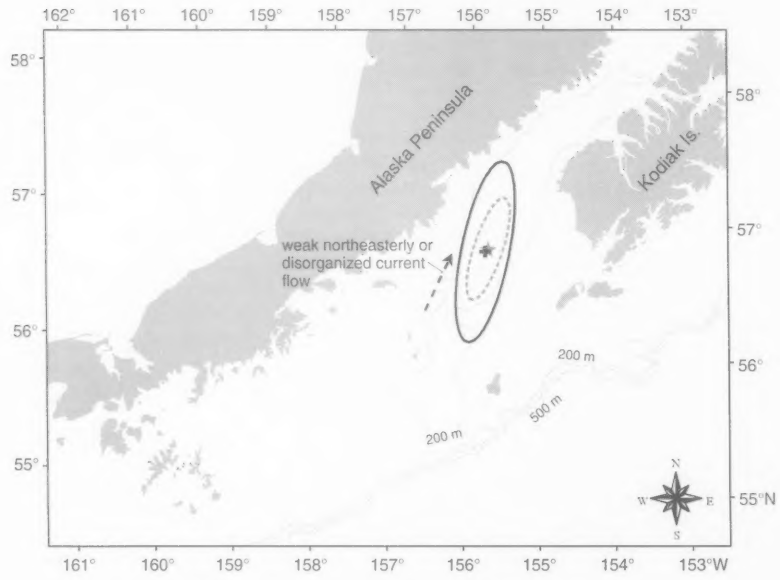
Laboratory observations of the changes in density of flathead sole eggs during development are inconsistent. Results of one study showed that egg density decreased throughout development to hatching (Alderdice and Forrester, 1974). Another study found that up to 24 hours before hatching the eggs floated at the surface of a container and then sank to the bottom and hatched (Miller, 1969), indicating that density had increased late in development. A field study of the vertical distribution of Atlantic halibut (*Hippoglossus hippoglossus*) eggs in Norwegian fjords showed that later stage eggs had a higher density (and were found deeper) than earlier egg stages (Haug et al., 1986). Results from the present study support the findings of Miller (1969), in that the density of flathead sole eggs in the present study appeared to increase near the time of hatching. For the larvae of both the arrowtooth flounder (*Atheresthes stomas*) and Pacific halibut (*Hippoglossus stenolepis*), small larvae were found deep and larger sizes migrated towards the surface (Bailey and Picquelle, 2002). In the present study, flathead sole larvae had a similar vertical distribution pattern indicating that after hatching in deep water they rise to near the surface to feed.



✚ center of distributionof eggs in early May
★ center of distribution of larvae greater than 9 mm in late May (assumed to include larvae that hatched from early May eggs)

Figure 7

The drift of flathead sole (*H. elassodon*) larvae in Shelikof Strait during May 1994. Surface current flow was strong and southwesterly.



✚ center of distribution of all early May larvae (mean length 5.71 ±0.71 mm)
★ center of distribution of late May larvae greater than 12 mm (assumed to include larvae present in early May)

Figure 8

The drift of flathead sole (*H. elassodon*) larvae in Shelikof Strait during May 1996. Surface current flow was disorganized, or weak, and to the northeast.

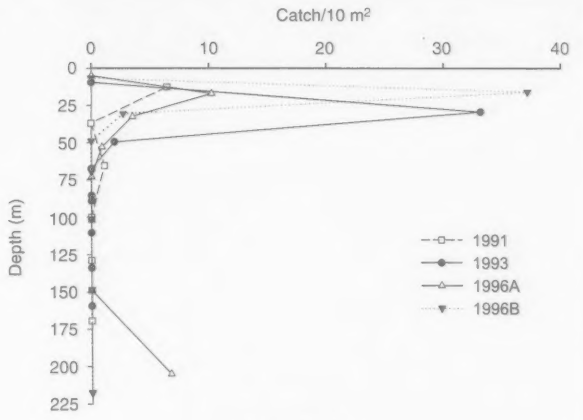


Figure 9

The vertical distribution of flathead sole (*H. elassodon*) larvae collected from four MOCNESS tows conducted in 1991, 1993, and 1996 during peak spawning. Symbols indicate the mean of the depth interval that the samples were collected in.

Some species of flatfish spawn offshore (e.g., arrowtooth flounder and Pacific halibut, Bailey and Picquelle, 2002), but the present study has shown that flathead sole spawn on the continental shelf. Flathead sole nursery areas have been found to be in the bays of the Alaska Peninsula and Kodiak Island (Norcross et al., 1999), and it is crucial that the larvae remain on the shelf near their nursery areas. Changes in egg density may be a mechanism for retaining flathead sole larvae on the shelf. For arrowtooth flounder and Pacific halibut larvae in the western Gulf of Alaska, it has been suggested that deep water currents (100–400 m depth in sea valleys and in troughs in the continental shelf) transport these larvae from the offshore areas where they hatch to their nearshore nurseries (Bailey and Picquelle, 2002). By sinking when they are nearing hatching, flathead sole eggs that have drifted southwesterly (i.e. away from nursery areas) with the surface currents can be brought back (along with newly hatched larvae) toward inshore juvenile nursery areas. Alternatively, the act of sinking as they near hatching may be a way for newly hatched larvae to avoid predation by keeping them out of the surface waters where they are likely to encounter predators. The physical environmental conditions of Shelikof Strait may also serve to retain flathead sole larvae on the shelf. In May 1994 when the Alaska Coastal Current flow was strong and to the southwest, larvae drifted southward but remained on the continental shelf. In May 1996 when the flow was weak, disorganized, and moving somewhat to the northeast, the larvae remained at virtually the same location for the entire month because surface current flow in Shelikof Strait was weakened and reversed because of anomalous atmospheric conditions. Under both flow regimes larvae remained on the continental shelf in southern Shelikof Strait. Eddies may also be an important retention mechanism for flathead sole larvae because entrainment in one of these could slow drift. Under typical conditions in Shelikof Strait (i.e., strong southwesterly current flow), eddies frequently occur and they drift slower than the water surrounding them (Kendall et al., 1996). They can also remain nearly stationary for two weeks (Schumacher et al., 1993). Both biological and environmental factors may work together to retain flathead sole larvae on the continental shelf and keep them near their nursery areas.

Acknowledgments

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Movements and spawning of white marlin (*Tetrapturus albidus*) and blue marlin (*Makaira nigricans*) off Punta Cana, Dominican Republic

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Abstract—With a focus on white marlin (*Tetrapturus albidus*), a concurrent electronic tagging and larval sampling effort was conducted in the vicinity of Mona Passage (off southeast Hispaniola), Dominican Republic, during April and May 2003. Objectives were 1) to characterize the horizontal and vertical movement of adults captured from the area by using pop-up satellite archival tags (PSATs); and 2) by means of larval sampling, to investigate whether fish were reproducing. Trolling from a sportfishing vessel yielded eight adult white marlin and one blue marlin (*Makaira nigricans*); PSAT tags were deployed on all but one of these individuals. The exception was a female white marlin that was unsuitable for tagging because of injury; the reproductive state of its ovaries was examined histologically. Seven of the PSATs reported data summaries for water depth, temperature, and light levels measured every minute for periods ranging from 28 to 40 days. Displacement of marlin from the location of release to the point of tag pop-up ranged from 31.6 to 267.7 nautical miles (nmi) and a mean displacement was 3.4 nmi per day for white marlin. White and blue marlin mean daily displacements appeared constrained compared to the results of other marlin PSAT tagging studies. White marlin ovarian sections contained postovulatory follicles and final maturation-stage oocytes, which indicated recent and imminent spawning. Neuston tows (n=23) yielded 18 istiophorid larvae: eight were white marlin, four were blue marlin, and six could not be identified to species. We speculate that the constrained movement patterns of adults may be linked to reproductive activity for both marlin species, and, if true, these movement patterns may have several implications for management. Protection of the potentially important white marlin spawning ground near Mona Passage seems warranted, at least until further studies can be conducted on the temporal and spatial extent of reproduction and associated adult movement.

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White marlin (*Tetrapturus albidus*) and blue marlin (*Makaira nigricans*) are widely distributed throughout the tropical and temperate waters of the Atlantic Ocean and adjacent seas; the former species is endemic only to the Atlantic Ocean (Mather et al., 1975). Genetic analyses and tag recapture data have indicated that each species has a single Atlantic-wide population (ICCAT, 1998). Several stock assessment indicators indicate that the white marlin population has been severely overfished for several decades (ICCAT, 2001, 2002). The Atlantic blue marlin stock is also heavily over-exploited, but to a lesser degree. The main source of adult mortality for both stocks is the multinational offshore longline fisheries that, in the process of targeting tunas (Scombridae) and swordfish (*Xiphias gladius*), land the marlins as bycatch (ICCAT, 2002, 2003).

Despite their economic and ecological value, little is known about the biology and ecology of Atlantic marlins (Prince and Brown, 1991). This is especially true regarding the reproductive biology of white marlin and adult movement patterns in spawning areas (Baglin, 1979; Mather, 1975; White Marlin Status Review Team[1]; SEFSC[2]). Long-term (i.e., >40 years) commercial (Goodyear, 2003) and recreational (i.e., Cabeza de Toro Billfish Tournament, Graves and McDowell, 1995; Casilla[3]) fishing records indicate that, every spring, white marlin are present in relatively high numbers off the southeastern coast of Hispaniola. This observation, coupled with

[1] White Marlin Status Review Team. 2002. Atlantic White Marlin Status Review Document, 49 p. Report to National Marine Fisheries Service, Southeast Regional Office, 263 13th Avenue, St. Petersburg, FL 33701-5511.

[2] SEFSC (Southeast Fisheries Science Center). 2004. Atlantic Billfish Research Plan. National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149-1003.

[3] Casilla, W. 2003. Personal commun. Club Nautico de Santo Domingo, Calle Juan Baron Fajardo #2, Ensanche Iantini, Santo Domingo, Dominican Republic.

anecdotal information about gravid fish, prompted the present examination of adult movements in a potentially important, but as yet unconfirmed, spawning location.

The present study was conducted off Punta Cana, Dominican Republic, during April and May 2003. Objectives were 1) to characterize the horizontal and vertical movement of adult white marlin captured from the area using pop-up satellite archival tags (PSATs) and 2) to investigate by larval sampling, whether marlin were reproducing at this location.

Materials and methods

Deployment of PSAT tags on adult marlin was conducted from a 17-m charter fishing vessel by using standard trolling gear (9/0 long-shaft J hooks) and dead bait. Wildlife Computers Inc. (Redmond, WA) PAT 3 model tags were used. This tag allows the user to program pop-up date, sampling interval, criteria for premature release, bin demarcations for sampling temperature and pressure (depth), as well as transmission and memory priorities. These tags were programmed to sample depth (pressure), temperature, and light once every minute and the depth and temperature records were summarized into histograms at 3-hour intervals. A pressure-activated mechanical detachment device was also used which severs the monofilament tether at a depth of about 1500 m—well before the 2000 m depth at which the tag is crushed and disabled. This feature helps prevents data loss in the event of fish mortality.

All PSAT tags were rigged similarly according to methods described by Graves et al. (2002). Billfish handling and tagging procedures and associated devices reviewed by Prince et al. (2002a) were also used. The target area for tag placement was about 4 to 5 cm ventral to the dorsal midline, adjacent to the first several dorsal spines. An effort was made to insert the anchor through the dorsal midline, pterygiophores, and connective tissue to a depth just short of the anchor exiting the opposite side of the fish. In addition, a conventional streamer tag (series PS) was placed in the fish well posterior to the PSAT tag, according to standard procedures (Prince et al., 2002a).

Two devices were used during tagging which tend to reduce stress in captured fish and to aid in proper tag placement. The first was a "snooter" (a wire snare housed in a 1.5-m PVC tube), which secures to the upper bill and allows the tagger to maintain control of the fish while its head remains beneath the water during the tagging procedure (Prince et al., 2002a). The second was a small hook "gaff" (a long shaft 9/0 hook with point and barb removed) to manipulate the position of the fish in relation to the tagging vessel. Captured fish were resuscitated for 3 to 15 minutes, depending on their apparent state of exhaustion, by moving the vessel ahead at two to three knots while maintaining control of the fish with the snooter. State of exhaustion was inferred from coloration, fight time, and signs of sluggish movement.

One white marlin died during tagging and was retained for examination of its reproductive status. Whole or quarter transverse sections of ovarian tissue were preserved in 10% formalin. Preparation for histological analysis followed McBride et al. (2002). Histological determination of spawning activity was based on oocyte classification and the presence of postovulatory follicles (Wallace and Selman, 1981; Hunter and Macewicz, 1985; Hunter et al., 1992).

Once adult marlins were located for tagging, neuston sampling was conducted from the same fishing vessel with methods similar to those reported by Serafy et al. (2003). In the present study, ten-minute daytime tows were performed with two neuston nets. Both nets had 1000-μm mesh and were attached to 1 m$\times$0.5 m or 2 m$\times$1 m rectangular aluminum frames. Water volume filtered was measured with a mechanical flow meter; station coordinates and water column depth measurements were obtained by using a hand-held geographical positioning system and depth sounder. Neuston collections were made along a series of transects that covered the general area of the recreational fishery for white marlin at this location (Fig. 1). The neuston samples were initially stored in 150 proof white rum. Upon returning to the laboratory (i.e., within 24–96 hours) they were transferred to 95% ethanol. Billfish larvae were sorted from the samples and measured by using Image Pro image analysis software (Image Pro Plus, version 4.5, Media Cybernetics, Inc. Silver Spring, MD). Larval identification was conducted by using restriction fragment length polymorphism analysis of the nuclear MN32-2 locus following the methods of McDowell and Graves (2002).

Results

Seven white marlin and one blue marlin were tagged with PSAT tags off Punta Cana, Dominican Republic, between April 23–24 and May 14–17 2003 (Table 1). All but two tags were programmed to pop-up after 30 days; the exceptions were 40-day deployments for one white marlin and one blue marlin. One of eight PSATs (deployed on a white marlin) failed to transmit data and one white marlin died prior to release (see below) from hook-related injuries. The displacements of the six white marlin from the original point of release ranged from 31.7 to 267.7 nmi (58.7 to 495.8 km), whereas the displacement for the blue marlin was 219.3 nmi (406.2 km, Table 1, Fig. 2). Displacements per day for white marlin ranged from 1.1 to 7.2 nmi (average of 3.4 nmi). Corresponding daily displacement for the one blue marlin was 5.48 nmi (Table 1).

The minimum and maximum depth and temperatures monitored for the seven PSAT-tagged marlin during the 30- and 40-day deployments showed that on most days, marlin visited depths ≥100 m (Fig. 3). Minimum temperatures ranged from 16.8° to 20.6°C, whereas the maximum temperatures ranged from 28.2° to 30.0°C. In all cases, the minimum depths for each fish monitored

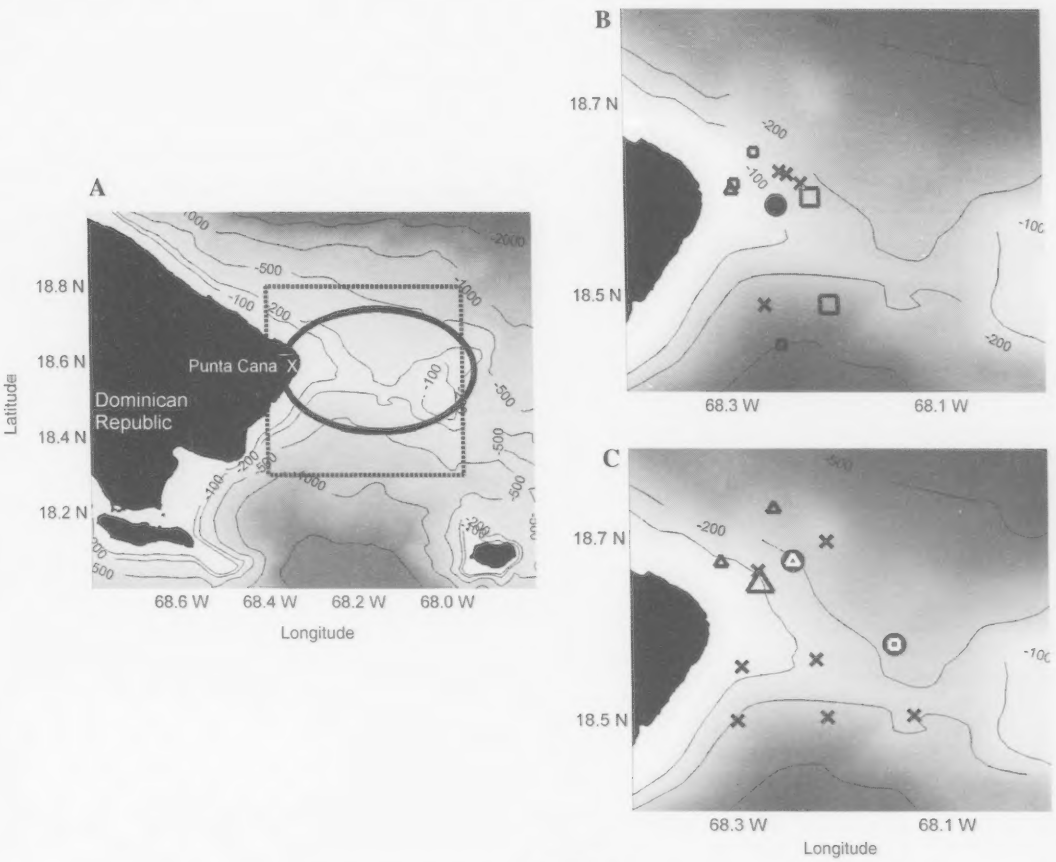

Figure 1

(**A**) Western part of Mona Passage off Punta Cana, Dominican Republic, showing the general area of the recreational fishery for white marlin (*Tetrapturus albidus*, rectangle) and larval sampling (oval); (**B**) April 23–24 sampling stations and (**C**) May 13–17 sampling stations. × = stations with no billfish larvae. □ = stations with white marlin larvae, △ = stations with blue marlin (*Makaira nigricans*) larvae, ● = stations with unidentified larval istiophorids. Larger markers indicate two billfish in sample; smaller markers indicate one billfish in sample. Depth contours are in meters.

during April and May were recorded at the surface, whereas maximum depths ranged from 184 to 368 m (Fig. 3). In one case (i.e., PC-WHM01), the minimum and maximum temperatures and depths converged at the surface, indicating constrained vertical movement for this individual. However, in the majority of tracks there was a clear separation of minimum and maximum temperature and depth (e.g., PC-WHM02, Table 1), indicating that active vertical movements were made each day. Only one of the transmitting tags appeared to pop-up prematurely (PC-WHM01, Fig. 3). This tag disengaged from its white marlin host during a deep dive (368 m) after 28 days at large (two days early). Although the fate of this fish cannot be determined, death is a distinct possibility. In general, all marlin spent a high proportion of the time in which they were monitored in the upper 25 m and at temperatures ≥28°C. For example, marlin spent from 50% to 60% of the time in the first depth bin (0 to 25 m) and about 60% to 75% of their time in the 28° to 30°C temperature bin (Fig. 4). Both marlin species made dives down to 100–200 m or more on a fairly consistent basis but generally stayed at these depths less than 10% of the time (Fig. 4).

One female adult white marlin, measuring 157 cm lower jaw fork length, could not be resuscitated during pop-up satellite tagging, presumably because of damage caused by a hook that penetrated the stomach. Based on length-weight conversion equations (Prager et al., 1995), the estimated weight of this fish was 21.6 kg (47.2 pounds). The histologically examined ovaries contained distinct postovulatory follicles, indicating that spawning likely occurred within the previous 24 hours (Fig. 5, upper panel). In addition, imminent spawning (likely within the following 12 hours) was indicated by

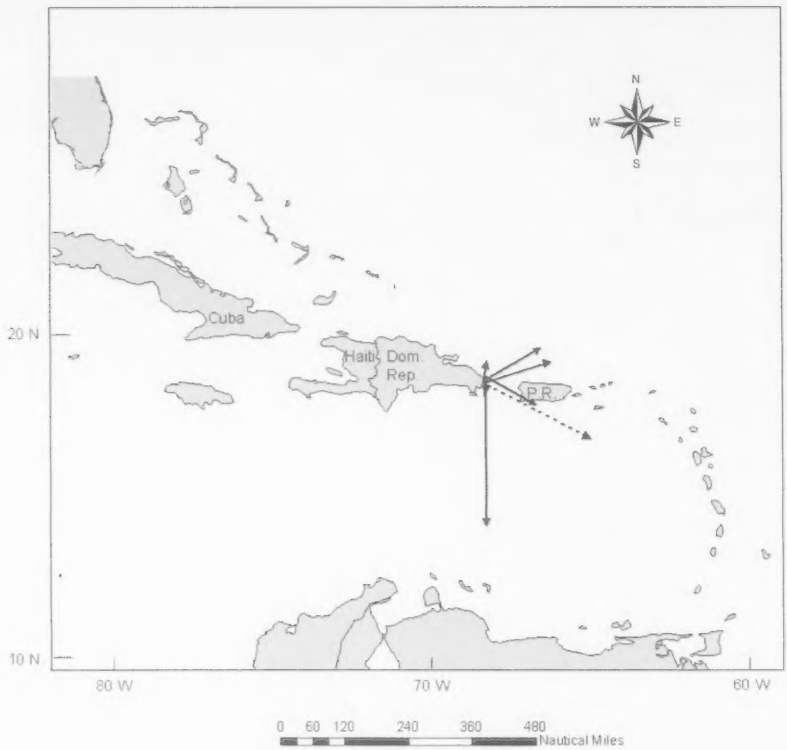

Figure 2

Displacement vectors (from point of tag release to point of tag pop-up in nautical miles, nmi) for six white marlin (*Tetrapturus albidus*) (solid lines, 31.7–268 nmi) and one blue marlin (*Makaira nigricans*) (dashed line, 219 nmi) released off Punta Cana, Dominican Republic, bearing pop-up satellite archival tags during April and May 2003. Tags were programmed for either 30- or 40-day deployments.

Table 1

Summary of pop-up satellite archival tag information for seven white marlin (*Tetrapturus albidus*, WHM) and one blue marlin (*Makaira nigricans*, BUM) released from recreational gear in the vicinity of Punta Cana, Dominican Republic, April and May 2003. Net displacements are given in nautical miles (nmi) and kilometers (km). Compass direction (in degrees) indicates the bearing from point of tag release to point of first transmission. Dashed line indicates that no value was available.

Tag number	Days monitored	Estimated weight pounds (kg)	Location of release	Location of first transmission	Compass direction	Net displacement nmi (km)	Displacement per day nmi (km)
PC-WHM-01	28	40 (18.14)	18.49°N, 68.38°W	19.17°N, 68.26°W	9.52°	41.21 (76.32)	1.47 (2.72)
PC-WHM-02	31	40 (18.14)	18.60°N, 68.27°W	19.56°N, 66.58°W	58.87°	111.87 (207.18)	3.61 (6.69)
PC-WHM-03	31	50 (22.68)	18.49°N, 68.37°W	19.14°N, 66.25°W	71.81°	126.76 (234.76)	4.09 (7.57)
PC-WHM-04	30	35 (15.88)	18.69°N, 68.27°W	18.16°N, 68.28°W	181.03°	31.68 (58.67)	1.06 (1.96)
PC-WHM-05	30	50 (22.68)	18.70°N, 68.29°W	17.81°N, 66.70°W	120.11°	105.22 (194.87)	2.84 (5.26)
PC-WHM-06	0	50 (22.68)	18.29°N, 68.13°W	—	—	—	—
PC-WHM-07	37	60 (27.22)	18.60°N, 68.30°W	14.12°N, 68.38°W	181.00°	267.73 (495.84)	7.24 (13.41)
PC-BUM-01	40	130 (58.97)	18.49°N, 68.38°W	16.75°N, 65.01°W	117.78°	219.32 (406.18)	5.48 (10.51)

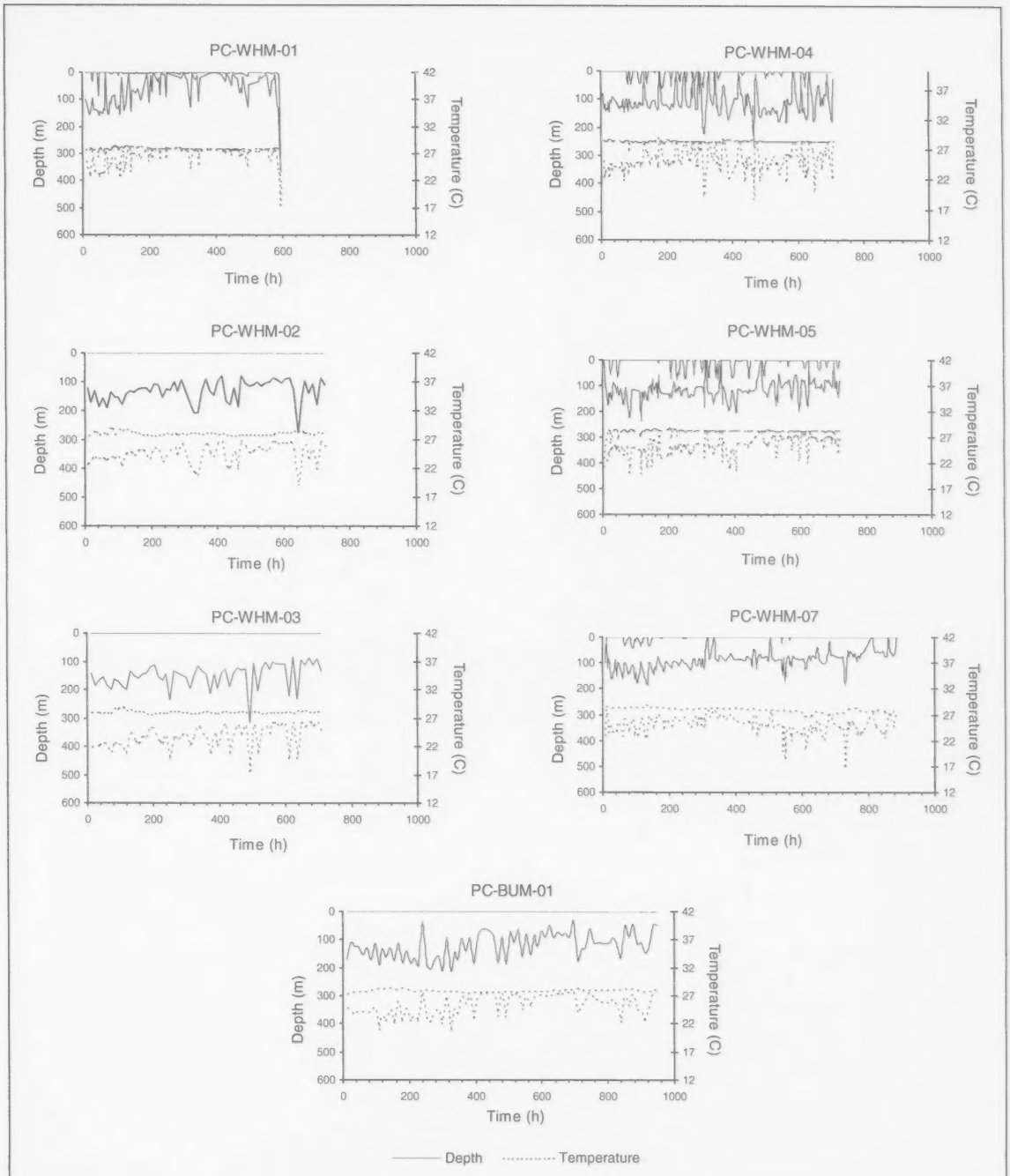

Figure 3

Minimum and maximum depth and temperature per 3-hour time intervals for six white marlin (*Tetrapturus albidus*) and one blue marlin (*Makaira nigricans*) monitored with pop-up satellite archival tags. Tags were programmed to deploy for either 30 or 40 days, April and May 2003, in the vicinity of Punta Cana, Dominican Republic. WHM=white marlin, BUM=blue marlin.

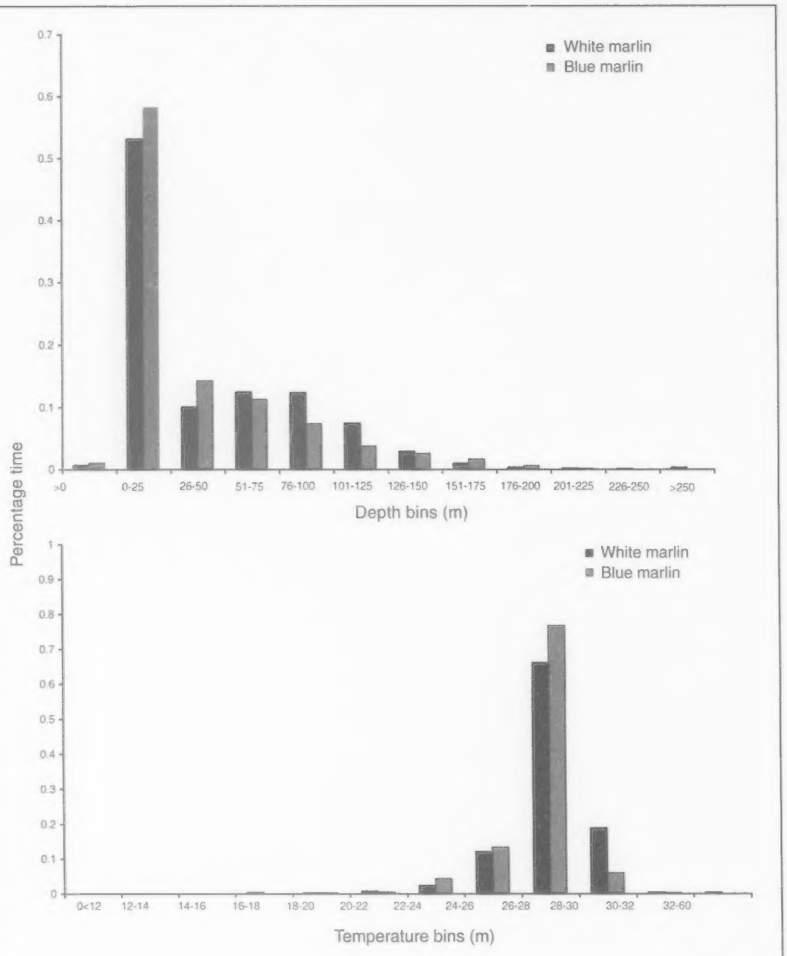

Figure 4

Total time at depth (upper panel) and time at temperature (lower panel) for white marlin (*Tetrapturus albidus*) and blue marlin (*Makaira nigricans*) tagged with popup satellite archival tags during April and May 2003. Tags monitored marlin for 30 and 40 days.

some oocytes exhibiting an early state of final oocyte maturation, including migration of the nucleus towards the oocyte periphery and yolk coalescence (Fig. 5, lower panel).

A total of 23 neuston net tows were made in the general area of the recreational fishery from 23 April to 17 May 2003 (Fig. 1). These tows yielded 18 larval billfishes. Molecular identification was successful for 12 larvae: 8 white marlin and 4 blue marlin (Table 2). Half of the white marlin larvae were 3–4 mm standard length (SL), two were 4–5 mm SL, one was 6.2 mm SL, and one was 12.1 mm SL (Fig. 6). The one positively identified blue marlin larva captured in April was 4.6 mm SL; the remainder taken in May were 3.5 mm SL, 5.1 mm SL, and 10.4 mm SL. Sizes of the six unidentified billfish larvae ranged from 3 to 6 mm SL (Fig. 6).

Discussion

Larval sampling with neuston tows and histological analyses of adult ovaries confirmed spawning activity of white marlin in the vicinity of Punta Cana during April and May (2003). Co-occurrence of larval blue marlin and white marlin in samples indicated that the two species share this spawning location. White and blue marlin spawning activity in the vicinity of Punta Cana, as indicated from the data presented in our study,

also coincided in time and space with the fishing activity of the recreational white marlin fishery that has operated each spring at this location for over 40 years. From PSAT tag data, adult white and blue marlin caught at this time and in this area appeared to exhibit similar vertical and horizontal movement patterns in terms of time at depth, time at temperature, average horizontal displacement per day, net horizontal displacement, and direction of dispersion (compass heading).

Movements

Average displacement per day is one possible measure to characterize daily horizontal movement activity. We examined this metric in other PSAT studies on marlin and compared them with our results (Fig. 7). Graves et al. (2002) monitored eight blue marlin with PSAT tags caught off Bermuda in July 2000 for periods of 5 days each and reported net displacement vectors ranging from 7.8 to 26.4 nmi/day (mean displacement for the eight fish was 17.5 nmi/day). Kerstetter et al. (2003) also monitored blue marlin during the summer months with PSAT tags in the northwest Atlantic (for 5 and 30 days) and found that displacements ranged from 15.1 to 39.2 nmi/day (mean for six fish was 22.9 nmi/day). Net displacement findings (17.5 and 22.9 nmi/day), presumably for blue marlin spawning times (summer months) from these two studies were roughly 5 to 6.5-fold higher than the average displacements for white marlin reported in our present study (about 3.3 nmi/day) and were 3 to 4-fold higher than the average displacement for the one blue marlin monitored in our study (Fig.7). A recent report (Graves and Horodysky[4]) has provided displacement movements of white marlin monitored with PSAT tags for 5 to 10 day periods from three different areas in the Northwest Atlantic during May (Punta Cana, Dominican Republic), August–September (U.S. Mid-Atlantic waters), and November (La Guaira, Venezuela) 2002. Only the work in Punta Cana was conducted during the presumed spawning season for white marlin. Average displacements for these areas were 9.6

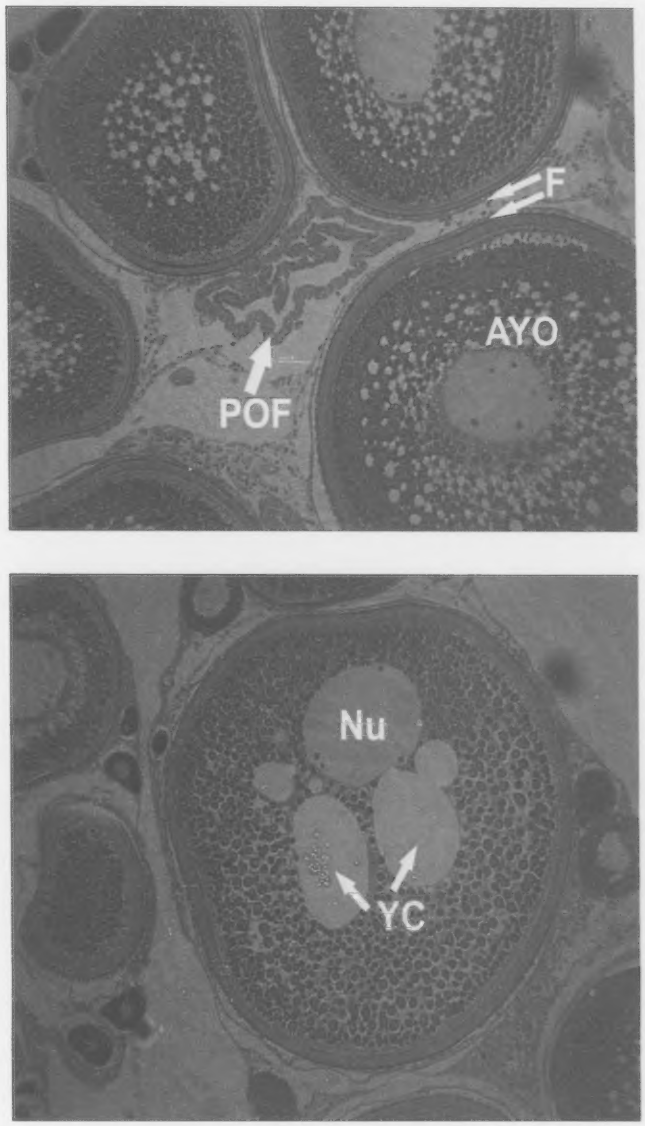

Figure 5

Upper panel. A postovulatory follicle (POF), advanced yolked oocyte (AYO), and follicle (F) are shown in section of gonad from a female white marlin (*Tetrapturus albidus)* sampled off Punta Cana, Dominican Republic, 16 May 2003. The presence of POFs indicates recent spawning (likely within 24 hours). **Lower panel.** The labeled oocyte has begun final oocyte maturation, as indicated by the migration of the nucleus (Nu) to the periphery and yolk coalescence (YC). Both of these steps are among the series of events initiated hormonally that occur just prior to spawning (likely within 12 hours).

[4] Graves, G. E., and A. Z. Horodysky. 2002. Progress report. Use of pop-up satellite archival tags to study survival and habitat utilization of white marlin released from the recreational fishery, 34 p. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062-1346.

Table 2

Summary of neuston tow information for larval collections of istiophorids in the vicinity of Punta Cana, Dominican Republic, April and May 2003. "Unidentified istiophorids" refers to specimens for which molecular identification was unsuccessful.

2003 dates	Number of tows	Volume filtered (m^3)	Number of positive tows	Number (length range) of white marlin	Number (length range) of blue marlin	Number (length range) of unidentified istiophorids
23–24 April	11	9400	7	7 (3.45–12.16 mm)	1 (4.6 mm)	2 (3.98–5.28 mm)
13–17 May	12	8413	5	1 (6.20 mm)	3 (3.49–10.45 mm)	4 (3.25–4.4 mm)
Total	23	17,813	12	8	4	6

nmi/day for Punta Cana; 9.4 nmi/day for the U.S. Mid-Atlantic region; and 8.2 nmi/day for La Guaira Bank (Fig. 7). Thus, the average white marlin displacements found by Graves and Horodysky were 2 to 3-fold higher than those reported in the present study. Black marlin (*Makaira indica,* Gunn et al., 2003) and striped marlin (*Tetrapturus audax,* Domeier et al., 2003) monitored mostly outside of spawning times and areas had displacements per day 2 to 4-fold higher than those in the present study. Therefore, reproductively active white marlin and blue marlin monitored in our study (30- or 40-day deployments) appeared to have more constrained average displacements per day than those in other studies where similar PSAT technology was used to monitor marlin in and outside of their respective spawning seasons.

Further PSAT-based research, with extended monitoring durations (i.e. at least ≥3–4 months) on white marlin and other billfish species in their spawning areas, will be necessary to clarify the causative factors for these findings. Interpretation of our findings also needs to be tempered by the fact that the displacement vectors (minimum straight line distances) used to characterize movements in this study were limited to beginning and end points. In theory, daily estimates of light-based geolocation would provide improved resolution of small-scale movement patterns. However, there is little scientific agreement (Musyl et al., 2001; Hill and Braun, 2001) as to the methods and validity of daily tracks generated from highly variable light levels, particularly for wide ranging species near the equator.

Although we present no evidence that the horizontal movement patterns of blue marlin (other than possibly constrained displacements) reported in our study are directly related to spawning activity, the possibility that white marlin could show fidelity to a spawning area cannot be ruled out. For example, Pepperell (1990) examined conventional tagging results off eastern Australia and reported that the periodic peaks in return frequency were possibly indicative of black marlin returning to the spawning ground as part of their annual migration cycle. The multidirectional pattern of blue and white marlin displacements found in the present study was very similar to the pattern reported by Graves et al. (2002) for blue marlin monitored with PSAT tags for five days off Bermuda. The relatively short-term duration of PSAT tags in both studies (5–40 days) generally precludes detection of directed seasonal horizontal movement patterns (including potential annual fidelity to a spawning area) as described by Mather et al. (1975), Pepperell (1990), and Ortiz et al. (2003).

Detailed accounts of temperature and depth preferences of electronically monitored white marlin have been rare and those that do exist are limited to very short (≤ten days) monitoring durations (Block et al., 1990; Horodysky et al., 2003; Graves and Horodysky[4]). We found that white marlin monitored with PSATs for periods of 28–40 days spent the majority of time in the upper 25 m of the water column at temperatures of 28–30°C. Similar findings were found for this species by Graves and Horodysky[4] and Horodysky et al. (2003), as well as for blue marlin, black marlin, and striped marlin reported by Graves et al. (2002); Kerstetter et al. (2003); Gunn et al. (2003); and Domeier et al. (2003). However, we could not directly address the depth at which spawning occurs in our study from PSAT results, other than to note the preference of adults for, and capture of larvae in, surface waters. Empirical data on the depth of spawning for istiophorids are not available, although anecdotal evidence indicates that some species may spawn in surface waters (black marlin observations by Harvey, personal commun.[5]).

Spawning

Prior studies of gonads have indicated that white marlin spawn in the northwest Atlantic during the spring (Baglin, 1977, 1979; de Sylva and Breder, 1997). Spring aggregations of white marlin have been the target of the Cabeza de Toro billfish tournament off Punta Cana for over 40 years (Casilla[3]), and the sampling of larvae in

[5] Harvey, G. C. McN. 2004. Personal commun. 102 Webster Drive, P.O. Box 10499 APO, Grand Cayman Island, Cayman Islands, British West Indies.

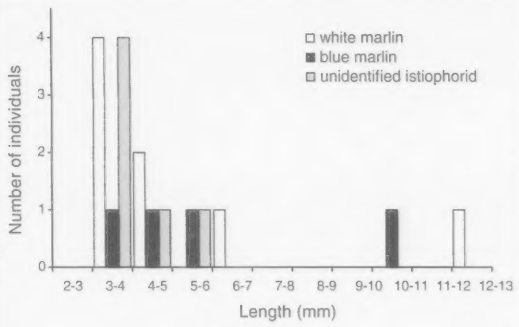

Figure 6

Length-frequency distribution for larval white marlin (*Tetrapturus albidus*), blue marlin, (*Makaira nigricans*), and unidentified istiophorids collected in the vicinity of Punta Cana, Dominican Republic, April and May 2003.

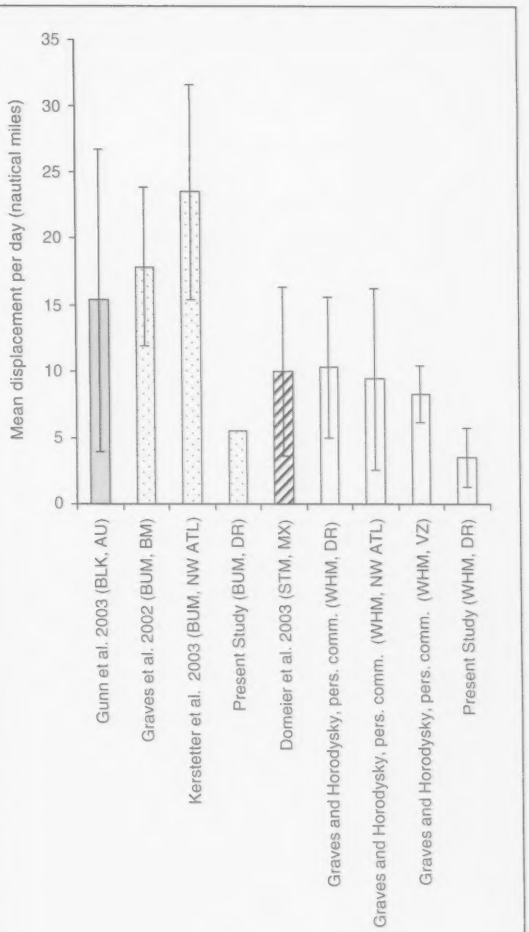

Figure 7

Mean displacement per day (in nautical miles) for blue marlin (*Makaira nigricans*), white marlin (*Tetrapturus albidus*), black marlin (*Makaira indica*), and striped marlin (*Tetrapturus audax*) monitored with pop-up satellite archival tags by Gunn et al. (2003) [Australia], Domeier et al. (2003) [Mexico], Graves et al. (2001) [Bermuda], Kerstetter et al. (2003) [Northwest Atlantic], Graves and Horodysky[4] [Punta Cana, Dominican Republic, La Guaira, Venezuela, U.S. Mid-Atlantic region], and present study. In all studies, displacements were computed from the point of tag release to the point of first transmission from PSAT tags and are not meant to infer tracks taken by the fish. Means are accompanied by ± one standard deviation for each species identified as follows: blue marlin (BUM, stippled bar), white marlin (WHM, empty bar), black marlin (BLK, solid bar), and striped marlin (STM, cross hatched bar).

the present study is the first to provide direct evidence of springtime spawning activity in this area. Histological assessment of the captured female ovarian tissue is consistent with the premise that the adult white marlins in the aggregation that we located during fishing and PSAT tagging operations participated in spawning activity. This contention is strengthened by the presence of very small, presumably very young, white (and blue) marlin larvae in the same location.

The presence of larvae is the most direct way of documenting that a spawning event has actually occurred. This is particularly relevant to highly mobile species, such as billfishes, that can cover large distances in a short time (Prince and Brown, 1991). Serafy et al. (2003) used a similar approach to identify blue marlin spawning grounds in the area of Exuma Sound, Bahamas. In their neuston collections, 90 blue marlin, no white marlin, and three sailfish larvae were captured. Because Serafy et al., (2003) sampled during the entire month of July, it seems possible that larval sampling in Exuma Sound took place after the majority of white marlin spawning had already occurred. Subsequent neuston sampling of Bahamian waters yielded white marlin larvae in Exuma Sound in April and in the Old Bahama Channel and just east of Long Island in March, but no blue marlin during these months (D. E. Richardson and S. A. Luthy, unpubl. data). Extensive sampling of the Straits of Florida (SOF) over four years resulted in sporadic captures of white marlin larvae in May and June. Blue marlin was the more common larval marlin in the SOF and was captured from June to September (S. A. Luthy, unpubl. data). In the present study, white marlin larvae were twice as abundant in larval samples as blue marlin larvae (which had been captured earlier in Punta Cana) than in other areas where blue marlin larvae had been found. These results are consistent with reports that white marlin is primarily a spring-time spawner but mark an expansion of the July to October spawning season reported for blue marlin in the North Atlantic by Erdman (1968) and de Sylva and Breder (1997).

For blue marlin larvae <6.2 mm SL, Serafy et al. (2003) found problems with estimating age from size with the larval growth equations reported by Prince et al. (1991). Serafy et al. (2003) suggested an exponential growth curve with an assumed size-at-hatching of 2.5 mm SL yielded more realistic larval age values for this growth stanza (<6.2 mm SL). Application of the Serafy et al. (2003) growth model to the larval blue marlin collected in the present study indicates that larvae 3 mm SL were 2 days old, 4-mm-SL larvae were 5 days old, and 5-mm-SL larvae were over 7 days old. It seems possible that blue and white marlin have similar size-at-hatching and growth rates at this early stage of development. Given this assumption, the fact that half of the white marlin larvae (4 out of 9) and a third of the blue marlin larvae sampled in this study were 3–4 mm long (i.e., only a few days old) indicates that spawning activity was taking place in the same general area where these larvae were captured and where the recreational fishery for these species was being pursued. This statement may not hold true for the larval marlin in our collections over 4 mm SL because increases in size and age add increased uncertainties concerning possible spawning locations. Providing a more precise estimate of spawning location was beyond the scope of our study, although we would expect that the upstream spawning locations (assuming minimal mobility of larvae) of both marlin species to be a function of the prevailing currents and oceanographic features in the Punta Cana area and the elapsed time between the spawning event and sample collection. Future research should focus on a more rigorous and comprehensive estimate of spawning location for all sizes and ages of larvae. This would require both a significant increase in the spatial and temporal larval sampling scheme, as well as direct aging methods for both species and sizes of marlin larvae collected.

Implications for managment and future research

The current stock status of Atlantic white marlin indicates that biomass is only at about 12% of the level necessary to maintain maximum sustainable yield (MSY) and continues to decline (ICCAT, 2002). The stock has been estimated to be incurring fishing mortality at a rate about eight times higher than the population can sustain to produce MSY (ICCAT, 2002). Although the Atlantic blue marlin stock is also considered to be overexploited, its status is not as precarious as that of white marlin (ICCAT, 2001). The characterization of adult movements and larval distribution in a potentially important spawning area is seen as a necessary "first step" toward improved management and rebuilding of depressed Atlantic billfish stocks, possibly with gear restrictions (e.g., use of circle hooks, Prince et al., 2002b; Horodysky and Graves, 2005). Improved management seems particularly relevant in the area of Punta Cana because the target of the 40-year-old Cabeza de Toro tournament is, and probably always has been, a reproductively active aggregation of white marlin. In light of the ICCAT recommendation to reduce mortality on the overexploited marlins from all Atlantic fisheries (ICCAT, 2002), a shift to catch-and-release requirements for the white marlin recreational fishery off Punta Cana, and the use of circle hooks during the spring months, may be suitable options. In terms of spawning, there is an obvious need for more detailed spatiotemporal information on the distribution of marlin reproduction and on the identification of nursery areas to help managers make informed decisions regarding conservation of the resource. In addition, more fine-scale data on adult movement patterns in relation to horizontal and vertical use of the water column, including identification of spawning depth, are necessary.

Acknowledgments

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Life history characteristics for silvergray rockfish (*Sebastes brevispinis*) in British Columbia waters and the implications for stock assessment and management

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Abstract—We summarize the life history characteristics of silvergray rockfish (*Sebastes brevispinis*) based on commercial fishery data and biological samples from British Columbia waters. Silvergray rockfish occupy bottom depths of 100–300 m near the edge of the continental shelf. Within that range, they appear to make a seasonal movement from 100–200 m in late summer to 180–280 m in late winter. Maximum observed age in the data set was 81 and 82 years for females and males, respectively. Maximum length and round weight was 73 cm and 5032 g for females and 70 cm and 3430 g for males. The peak period of mating lasted from December to February and parturition was concentrated from May to July. Both sexes are 50% mature by 9 or 10 years and 90% are mature by age 16 for females and age 13 years for males. Fecundity was estimated from one sample of 132 females and ranged from 181,000 to 1,917,000 oocytes and there was no evidence of batch spawning. Infection by the copepod parasite *Sarcotaces arcticus* appears to be associated with lower fecundity. Sexual maturation appears to precede recruitment to the trawl fishery; thus spawning stock biomass per recruit analysis (SSB/R) indicates that a $F_{50\%}$ harvest target would correspond to an F of 0.072, 20% greater than M (0.06). Fishery samples may bias estimates of age at maturity but a published meta-data analysis, in conjunction with fecundity data, independently supports an early age of maturity in relation to recruitment. Although delayed recruitment to the fishery may provide more resilience to exploitation, managers may wish to forego maximizing economic yield from this species. Silvergray rockfish are a relatively minor but unavoidable part of the multiple species trawl catch. Incorrectly "testing" the resilience of one species may cause it to be the weakest member of the species complex.

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Silvergray rockfish (*Sebastes brevispinis*) range from the Gulf of Alaska to central Baja California (Love et al., 2001) and are a minor part of the trawl and hook-and-line fisheries catch from northern Washington to the Gulf of Alaska (Alaska Fisheries Information Network,[1] Pacific Fisheries Information Network,[2] Pacific Biological Station[3]). Coastwide commercial landings averaged 2600 metric tons (t) from 1990 to 2000, and about two-thirds of these landings came from British Columbia (B.C.) waters, mostly from bottom trawling. Hook-and-line landings are the most common type in Alaskan waters (mostly from southeastern Alaska) and have averaged less than 20 t. Combined annual trawl landings from Washington and Oregon peaked at over 1000 t from 1977 to 1979, declined to an average of 210 t from 1990 to 1998, and since 1999 have further declined to negligible levels.

The B.C. bottom trawl fishery is currently managed through individual vessel quotas (IVQs) whereby a fixed proportion of the annual quota for each stock is allocated to each quotaholder. Because silvergray rockfish are currently assessed and managed as four separate stocks (Fig. 1: Pacific Marine Fisheries Commission areas 3CD, 5AB, 5CD, and 5E), a vessel may possess up to four area-specific quotas for silvergray rockfish. All bottom trawlers on the outer coastal waters of British Columbia are required to have an independent observer on the vessel. Once vessels have reached their IVQ for one area and species, and have exhausted their limited opportunity to temporarily lease quota from other lease-holders, they must cease all bottom trawling even though they may still have IVQ remaining for other species in that area.

The quotas for silvergray rockfish are relatively small compared with those for other species in the fishery; thus fishermen can fully fill their silvergray rockfish IVQs as they target other species. However, if silvergray rockfish become difficult to avoid through increased abundance or availability, or if the silvergray rockfish quota is reduced, even though catch rates remain constant, they become a nuisance in that fishermen cannot fulfill their IVQs for other species without exceeding their silvergray rockfish IVQ. Therefore, the quotas for minor species, such as silvergray rockfish, now assume more importance than would be gained from their landed value. Finally, the enactment of species-at-risk legislation in Canada has led to the requirement

[1] Alaska Fisheries Information Network. 2000. AKFIN Support Center, 612 W Willoughby Ave. Suite B. Juneau, Alaska 99801.

[2] Pacific Fisheries Information Network. 2000. Pacific States Marine Fisheries Commission, 205 SE Spokane Street, Suite 100, Portland, Oregon 97202.

[3] Pacific Biological Station. 2000. Unpubl. data. Fisheries and Oceans Canada. Nanaimo, British Columbia V9T 6N7, Canada.

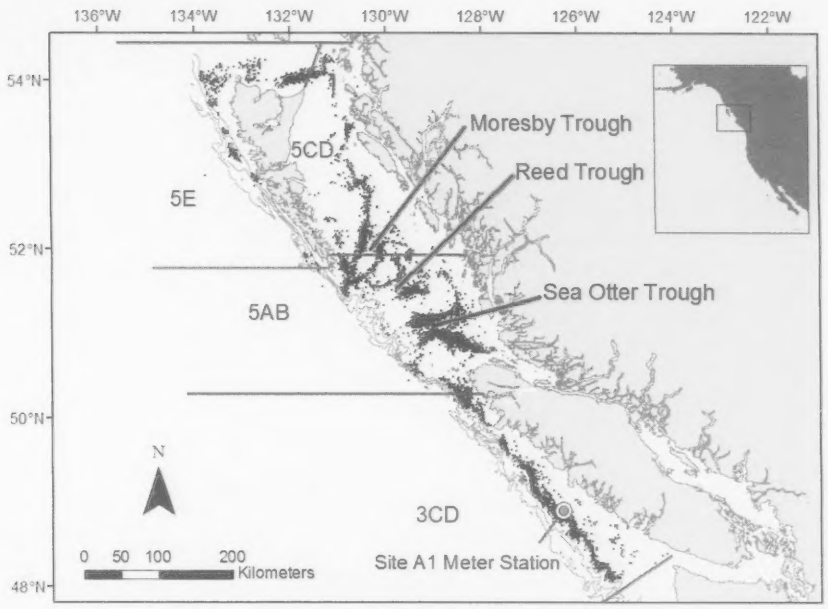

Figure 1

Coastal waters of British Columbia showing boundaries of silvergray rockfish (*Sebastes brevispinis*) stocks, trawl capture locations of silvergray rockfish (black dots) for 1996–2000, mooring site for the oceanographic metering of temperature at-depth (A1 meter station), and 500-, 1000-, and 1500-m depth contours.

to assess and protect the status of any species affected by fishing, regardless of its commercial value.

Research on silvergray rockfish is an example of an area that has been neglected owing to the lack of economic importance of this species in the commercial fisheries. Even the data that are available have been collected incidentally during fishing operations targeting other species or during generic sampling programs. Nevertheless, we show in the present article that these data, in conjunction with detailed commercial catch and effort data, can be used to provide insight into the biology, assessment, and management of silvergray rockfish. This article summarizes this information and provides estimates of the various life history parameters needed for stock assessment. Some of the estimates represent updates from previous work, but we also for the first time present estimates of fecundity and maturity at age and size. Using these values, we also derive a target reference point.

Materials and methods

Data sources

Data for silvergray rockfish were collected from B.C. waters during port sampling, at-sea observer programs, and research cruises from 1977 through 2000. These data reside at the Pacific Biological Station, Nanaimo, B.C., Fisheries and Oceans, Canada. As of June 2000, the database contains information on over 40,000 specimens. Of these specimens, we aged 13,671 representing most of the specimens from which we obtained otoliths, in addition to documenting length, sex, and maturity stage. We, also used catch observations from the commercial trawl observer program from 1996 through 2000.

Habitat

Preferred depth distributions of silvergray rockfish were inferred from analyzing catch rates in the commercial data. We used all bottom tows that contained silvergray rockfish and included tow duration. Bottom depth of the tows was determined as the midpoint between beginning and end depth of the tows. We applied a nonparametric locally weighted regression smoothing function (LOESS) (Cleveland, 1979) to log-CPUE observations grouped by 20-m intervals.

Depth of peak catch rates by month were compared with temperature-at-depth estimates based on data collected from the site A1 meter station on the west coast of Vancouver Island (Fig. 1: 48°32″N by 126°12″W). These data, collected from 1986 to 2000 (excluding El Niño years), were taken from 35-, 100-, 175-, and 400-m depths. The temperatures at fixed depths were then

Table 1

Field classification of gonad maturity stages for silvergray rockfish (*Sebastes brevispinis*) used by the Groundfish Section, Pacific Region Science Branch, Fisheries and Oceans, Canada.

	Female ovaries	Male testes
1	Immature (translucent, small, color can be clear, amber, yellow, or pink)	Immature (translucent, string-like)
2	Developing (small, opaque or translucent, can be yellow, usually light pink)	Developing (swelling, brown-white)
3	Developed (eggs usually white or cream white, can be yellow or orange-yellow)	Not used
4	Fertilized (large, cream or orange-yellow eggs, translucent)	Developed (large, white, easily broken)
5	Embryos or larvae present (includes eyed eggs)	Ripe (running sperm)
6	Spent (flaccid, red, a few larvae may be present)	Spent (flaccid, creamy-brown, some milt present but not free-flowing)
7	Resting (moderate size, firm, red-grey, red-grey, pink, or purple to almost black)	Resting (ribbon-like, small brown)

converted through interpolation to provide depth at specific temperatures (Hourston[4]).

Aging and growth determinations

Ages were determined by using the otolith burnt-section technique (MacLellan, 1997) with a minor modification. A survey directed at studying juvenile rockfish in 1991 captured two 17-cm silvergray rockfish. An examination of these otoliths indicated that the previous application of the method had incorrectly assigned the first annulus to the age count in specimens. Therefore, some previously aged specimens were probably under-estimated by one year (MacLellan[5]). A faint first annulus is consistent with the late spring to mid-summer parturition of silvergray rockfish that appears to preclude significant summer growth in its first year. The method was modified in August of 1992, and we added one year to all previously aged specimens in the data set.

Most (85%) of the otoliths were aged by one reader. The remaining 15% were aged by two readers to monitor consistency. If there was a disagreement, the two readers agreed on a "resolved" age.

Age and length data were fitted to a generalized growth model (Schnute, 1981) (Appendix 1). Growth dimorphism was calculated as the ratio of the midpoints of fork length (maximum observed length minus minimum observed length) between males and females (Lenarz and Wylie Echeverria, 1991).

Reproductive maturity

Maturity stage was classified macroscopically in the field (Table 1). We examined the annual reproductive cycle by tracking the proportions in each maturity stage by month. Lacking histological confirmation for characterizing maturity, we followed the suggestion of Wylie Echeverria (1987) and used only those specimens collected from the reproductive or gestation period of March to August. Within this subset, we grouped female stages 1 and 2 as immature, and stages 3–7 as mature. Because most mature females exhibited fertilized eggs by March, we assumed that females with small, nondeveloped ovaries in March through August would not complete parturition in the same calendar year.

We assumed that stage 1, during which testes are translucent and string-like, was the only male immature stage. Subsequent stages 2 and 4–7 were grouped as mature (stage 3 was not used in the field). The proportion of stage-2 males (in relation to males in other mature stages) decreased rapidly during the mating season (September–January) indicating that many of the specimens classified as stage 2 would become mature within the same calendar year. We emphasize, however, that without histological support for these classifications, the assumptions of maturity-at-age or maturity-at-length remain tentative.

The estimated proportions of maturity at age were computed by fitting a generalized additive model (GAM) to the binomial maturity classes (0=immature, 1=mature) (Hastie and Tibshirani, 1990). A logistic link with a binomial error structure was applied, as well as a second-degree nonparametric LOESS smoother.

Fecundity

Fecundity was estimated from a single sample (n=132) of females captured by commercial bottom trawl in Sea Otter Trough in April 1989 (Fig. 1). The catch was stored in refrigerated seawater for four days prior to sampling. Sampling was stratified by length to obtain a range of ages, and from each fish we obtained measurements of fork length, gonad weight, and somatic weight. We also collected otoliths and counted the number of cysts con-

[4] Hourston, R. 2003. Personal commun. Institute of Ocean Sciences. Fisheries and Oceans Canada. 9860 West Saanich Road, P.O. Box 6000. Sidney, British Columbia. V8L 4B2, Canada.

[5] MacLellan S. 2000. Personal commun. Pacific Biological Station, Fisheries and Oceans Canada. Nanaimo, British Columbia. V9T 6N7, Canada.

taining the copepod parasite *Sarcotaces arcticus* in the coelomic cavity. All the oocytes of all the female gonads appeared to be in a prefertilized condition.

The ovaries that were used for fecundity estimation were fixed and stored in modified Gilson's solution (Leaman, 1988) and shaken weekly for one year. Fecundity estimates were derived gravimetrically (Leaman, 1988). Each ovary was drained and filtered through stacked sieves (100–750 μm); each clump was broken manually if possible. The ovarian membranes and connective tissue were teased away from eggs and discarded. The oocytes were transferred to millipore filters, vacuumed-dried for 15 minutes, and the oocytes and filter were weighed to 0.01 g. Four subsamples of approximately 0.1 g and 1000 oocytes were weighed to 0.0001 g. Total fecundity was estimated for each fish by multiplying total vacuum-dried ovary weight by the mean density of the four samples. Fecundity relationships against age, weight, and length were examined with a generalized additive model (GAM) (Hastie and Tibshirani, 1990). An identity link with a Gaussian error structure was used in each case. Ovaries to be used for histological examination were fixed in Smith's formal dichromate solution and then stored in 3% formaldehyde. Histology samples were imbedded, sectioned, mounted, stained with Harris' haematoxylin, and counterstained with alcoholic eosin (Gray, 1954).

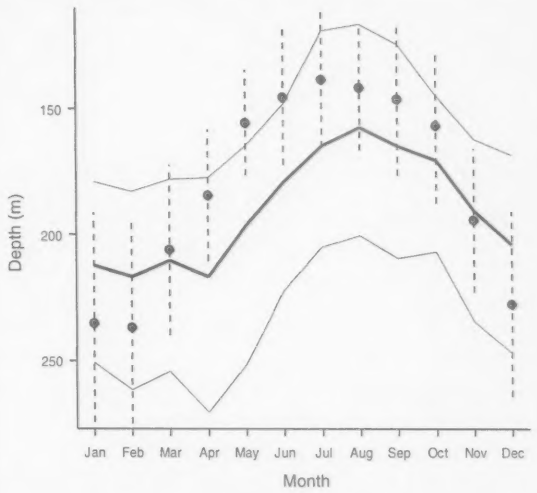

Figure 2

Silvergray rockfish (*Sebastes brevispinis*) seasonal depth distribution. The solid lines show the median (heavy line) and 25th and 75th percentiles (thin lines) for the number of silvergray rockfish catch observations (observed commercial trawl sets) at depth, between 1996 and 2003. The dots indicate the estimated depth at 7.2°C ±1 standard deviation (dotted line).

Spawning stock biomass per recruit (SSB/R)

We combined estimates of instantaneous natural mortality rate (M) of 0.06 and partial recruitment from Stanley and Kronlund (2000) with our estimates of the proportion mature at age and predicted fecundity at age in order to derive estimates of the expected population fecundity of unfished populations (Appendix 2). The impact of fishing on spawning stock biomass per recruit (SSB/R) can then be explored by comparing the ratio of predicted cumulative fecundity of a cohort under exploitation to predicted cumulative fecundity under no fishing pressure (Gabriel et al., 1989; Clark, 1991).

Results

Habitat

The commercial data indicated that the highest catch rates and most of the landings of silvergray rockfish come from the edge of the continental shelf or along the edges of deep troughs (Fig. 1). These tows were typically conducted in bottom depths of 100 to 300 m, although silvergray rockfish have been reported from tows with mid-point bottom depths greater than 580 m. Monthly catch rates by depth indicate a seasonal trend wherein peak catch rates are highest in depths of 180–280 m in March and April, but highest in depths of 100–200 m in September and October (Fig. 2).

If the shift in catch rates correctly indicates seasonal movement, and the interpolated temperatures at site A1 characterize bottom temperatures on the coast, together they indicate that silvergray rockfish tend to maintain peak densities at bottom water temperatures centered around 7.2°C (Fig. 2). The move to shallower water in the late spring, however, seems to lag behind the cooling of shallower water that results from summer upwelling (Thomson[6]). The return to deeper water in the fall is coincident with the warming of water at greater depths.

The cohabitants of silvergray rockfish were also inferred from commercial trawl observations. For these data, we selected tows with at least 50 kg of silvergray rockfish. Silvergray rockfish represented 12.8% of the total catch of over 36,000 t (Table 2). The dominant species by weight in these tows were Pacific ocean perch (*Sebastes alutus*), arrowtooth flounder (*Atheresthes stomias*), yellowmouth rockfish (*S. reedi*), yellowtail rockfish (*S. flavidus*), redstripe rockfish (*S. proriger*), and canary rockfish (*S. pinniger*). The species most frequently co-occurring in the tows were arrowtooth flounder, lingcod (*Ophiodon elongatus*), spiny dogfish

[6] Thomson, R. 2003. Personal commun. Institute of Oceans Sciences, Fisheries and Oceans Canada. 9860 West Saanich Road, P.O. Box 6000. Sidney, British Columbia V8L 4B2, Canada.

Table 2

Fish species captured in 1996–99 B.C. bottom trawl tows that contained silvergray rockfish (*Sebastes brevispinis*).

Common name	Species	% of total catch (36,489,773 kg)	% frequency (10,820 tows)
Silvergray rockfish	*Sebastes brevispinis*	12.8	100.0
Arrowtooth flounder	*Atheresthes stomias*	13.0	77.2
Lingcod	*Ophiodon elongatus*	2.8	65.1
Spiny dogfish	*Squalus acanthias*	2.5	58.4
Yellowtail rockfish	*Sebastes flavidus*	11.3	57.4
Canary rockfish	*Sebastes pinniger*	5.4	55.2
Redstripe rockfish	*Sebastes paucispinis*	1.3	54.0
Pacific cod	*Gadus macrocephalus*	1.1	53.7
Pacific halibut	*Hippoglossus stenolepis*	0.6	48.2
Redstripe rockfish	*Sebastes proriger*	7.2	47.3
Rex sole	*Errex zachirus*	0.8	46.6
Sablefish	*Anoplopoma fimbria*	0.6	46.2
Spotted ratfish	*Hydrolagus colliei*	0.6	43.7
Pacific ocean perch	*Sebastes alutus*	13.9	40.4
Yellowmouth rockfish	*Sebastes reedi*	12.7	39.2
Dover sole	*Microstomus pacificus*	1.1	36.0
Petrale sole	*Eopsetta jordani*	0.4	34.5
Redbanded rockfish	*Sebastes babcocki*	0.9	33.7
English sole	*Pleuronectes vetulus*	0.5	28.3
Widow rockfish	*Sebastes entomelas*	3.9	27.1
Greenstriped rockfish	*Sebastes elongatus*	0.3	27.0
Longnose skate	*Raja rhina*	0.3	26.0
Others		6.2	—

(*Squalus acanthias*), yellowtail rockfish, canary rockfish, redstripe rockfish, and Pacific cod (*Gadus macrocephalus*). All of these species were observed in more than 50% of the selected tows.

The cohabitants varied with depth. Tows conducted in depths less than 200 m tended to include lingcod, dogfish, canary rockfish, and yellowtail rockfish, whereas catches from greater than 200 m were dominated by arrowtooth flounder, Pacific ocean perch, redstripe rockfish, and yellowmouth rockfish. Fishermen report that silvergray rockfish are typically found over relatively "hard" bottom, often in proximity to bottom that was not trawlable because it was too rough. They are rarely caught in midwater trawls.

Aging and growth estimates

The maximum ages observed in Canadian samples were 81 and 82 years for females and males, respectively. The corresponding ages at the 99.9% percentiles were 76 and 77 years.

Although we assumed that our aging methods for silvergray rockfish provided unbiased estimates of age, agreement between readers was poor. Agreement to ±1 year was 60–80% for ages less than 20 years and then declined with age.

The standard errors of the growth parameter estimates show that there is a significant, albeit modest, difference in growth rates; females grow faster and to a larger size (Table 3, Fig. 3). Maximum observed length was 73 and 70 cm for females and males, respectively. We estimated the length-weight relationship for females and males separately and combined from 476 total specimens (Table 3, Fig. 3). The ratio of the midpoint lengths for males and females was 97.2 (Table 4), indicating little sexual dimorphism.

Maturation cycle

The field maturity observations were congruent for females and males (Fig. 4). Testes began developing (stage 2) in September and October and were large and swollen by November and December (stage 4) (Fig. 4). January and March testes were in the late stages of mating (stage 6), whereas from April through August testes appeared to be in a resting phase for males (stage 7). The few observations of large swollen testes with running sperm (stage 5) occurred from October through February. The

Table 3

Growth and fecundity parameter estimates and standard errors for silvergray rockfish (*Sebastes brevispinis*) (see Appendix 1 for parameter definitions).

		Females		Males		Combined	
Equation	Parameter	Estimate	SE	Estimate	SE	Estimate	SE
Length-at-age	y_1	48.985	0.048	47.887	0.041	48.468	0.034
	y_2	60.628	0.015	56.108	0.091	57.719	0.083
	a	0.0581	0.002	0.0708	0.002	0.0709	0.002
	b	1.0000		1.000		1.000	
	τ_1	15.000		15.000		15.000	
	τ_2	60.000		60.000		60.000	
Length/Weight (ln scale)	α	−4.000	0.137	−2.506	0.411	−3.634	0.157
	β	2.924	0.034	2.547	0.105	2.833	0.040
Fecundity/Somatic weight (ln scale)	α	3.014	0.572				
	β	1.367	0.073				
Fecundity/Length	α	−3.454	1.007				
	β	4.2833	0.251				

Table 4

Comparison of silvergray rockfish (*Sebastes brevispinis*) fork length ratio (group 1) with results from Lenarz and Echevarria (1991) (groups 2–4).

	Species group		Deep (>125m)	Shallow (≤125 m)	All rockfish species combined
1	Silvergray rockfish (present study)	Fork length ratio	0.97		
2	Water-column species	Number of species	12	5	17
		Standard length ratio	0.88	0.91	0.89
3	Demersal species	Number of species	5	12	17
		Standard length ratio	0.95	0.98	0.97
4	All rockfish species combined	Number of species	17	17	34
		Standard length ratio	0.90	0.96	0.91

peak period of mating is presumably December to February. One sample of 109 males, collected in March 1988, was recorded entirely as maturing. This one sample accounted for all but two records of stage-4 males collected in March and, therefore, contradicted the results of 20 other March samples, totalling 364 specimens. Although we found no evidence of a recording error, we suggest that these specimens were misclassified and were probably recovering instead of developing males.

The developing ovaries (stages 2 and 3), observed from January to April, shifted to fertilized through to resting stages (stages 3–7) in April to June. Eyed larvae were commonly observed from May to July although a few individuals with eyed larvae were observed in February, August, and October.

We examined whether there was a relationship between the size of the female and the timing of parturition by categorizing July observations as either "parturition not completed" (stages 3–5) or "parturition completed" (stages 6–7) (Fig. 5). The results indicated a dome-shaped relationship with length wherein it appears that a higher proportion of the smaller and larger females had not completed parturition. There were too few observations from June to examine the transition in more detail or to examine whether timing varied with latitude within B.C. waters.

Age observations from the commercial fishery indicate that both sexes are 50% mature at about 10 years of age and over 90% are mature at age 16 for females, and age 13 for males (Table 5, Fig. 6). However, the analysis was limited by the lack of young fish in the samples. For example, there were only five 8-year old and thirteen 9-year old females in the data set. Comparison of the age at maturity and partial recruitment at age indicates that silvergray rockfish mature prior to recruitment (Table 5, Fig. 7).

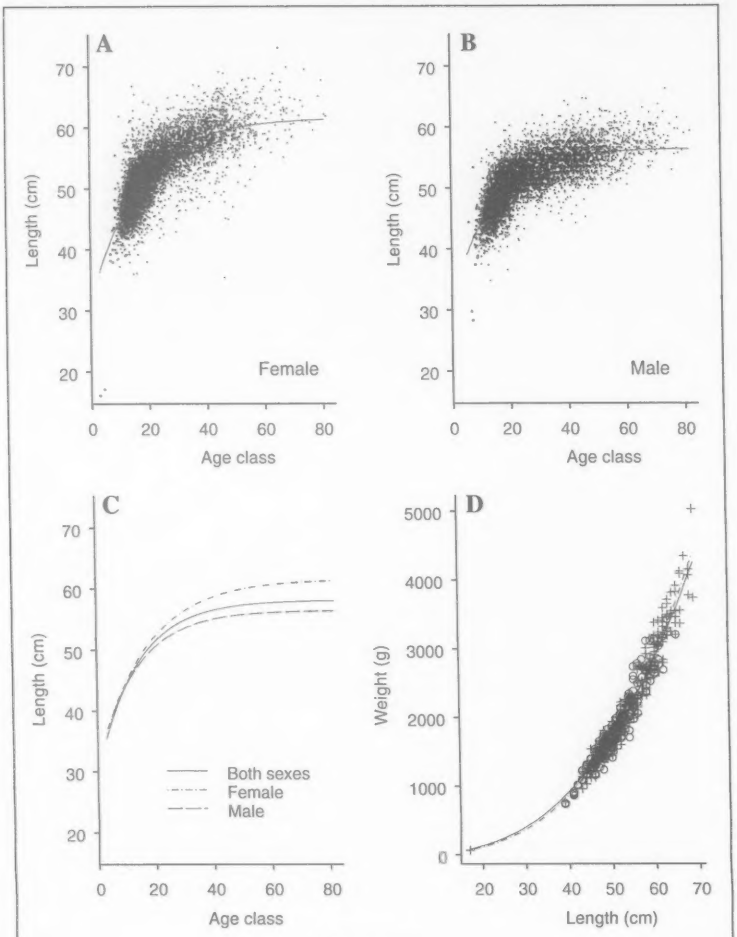

Figure 3

Observed lengths at age for (**A**) female and (**B**) male silvergray rockfish (*Sebastes brevispinis*). Predicted length-at-age for (**C**) females, males, and both sexes combined; and (**D**) weight at length for females ("+") and males ("○").

Fecundity and stock-assessment-parameter estimates

The total number of large oocytes ranged from 181,000 to 1,917,000 (Fig. 8). A general linear model (GLM) treatment of log fecundity against log somatic weight and age indicated that age was not a significant variable after accounting for somatic weight. Although size is a better predictor of fecundity than age, we also provide the predicted fecundity with age (Table 5) for subsequent calculation of SSB/R.

We examined histological cross-sections from 11 mature specimens in the sample. All appeared to be late in the process of vitellogenesis, the late stage 3 of Wylie Echeverria (1987) or stage V of Bowers (1992). The oocytes in each ovary were either large, with diameters ranging from 300 to 600 μm or smaller than 150 μ. There was little variation within ovaries in the diameter of the larger eggs ($\pm$ 50 μm) and thus no evidence of additional maturing batches.

The SSB/R analysis indicated that an instantaneous fishing mortality (F) that reduces the SSB/R to 50% of what could be expected with no fishing, ($F_{50\%}$) equates to an F of 0.072 (Fig. 9).

Discussion

Data sources

The opportunistic assemblage of samples collected from the commercial fishery and research cruises has two implications if one attempts to draw inference from these

data. The first is that while the overall number of samples and specimens is large, they are not equally distributed over time and space. Thus, for example, we cannot examine whether larger or older males complete the mating earlier in the season because of the lack of winter samples. The second implication is that the results are influenced by the fishing practices. This is particularly the case for inferring depth distribution from trawl catches.

Habitat

Silvergray rockfish appeared to be concentrated in the 100–300 m depth interval. Their distribution tended to overlap the distribution of "slope" and "shelf" assemblages of Weinberg (1994) that were based on survey results from northern California to southern British Columbia. The distribution also agrees with observations from research surveys in B.C. waters (Nagtegaal, 1983). Peak catch rate at depth indicates an annual depth migration, noted by fishermen, of about 80 m. The timing and range of this movement is considered by fishermen to be typical for rockfish (Dickens[7]).

The movement appears correlated with temperature. Bottom temperature increases in winter owing to downwelling (Fig. 2) (Thomson[6]). Thus, the shift to shallower water in the summer means that peak catch rates throughout the year are found in waters centered at just over 7°C. The apparent seasonal movement has obvious implications for stock assessments. Surveys designed to track abundance among years need to be consistent with respect to their timing and depth. More importantly, those who attempt to use CPUE to monitor abundance must consider changes in the distribution of fishing effort by season among years.

There has been no research on the larger scale movements of silvergray rockfish. Barotrauma induced during traditional trawl or hook-and line-fishing precludes tag-recapture studies, although recent work on other rockfish indicates there is potential for tagging *in situ* (Schrope, 2000; Starr et al., 2001). Nor do we know of any genetic studies on silvergray rockfish to determine stock structure, although the

[7] Dickens, B. 2000. Personal commun. 1678 Admiral Tryon Boulevard. Qualicum Beach, British Columbia V0R 2T0, Canada.

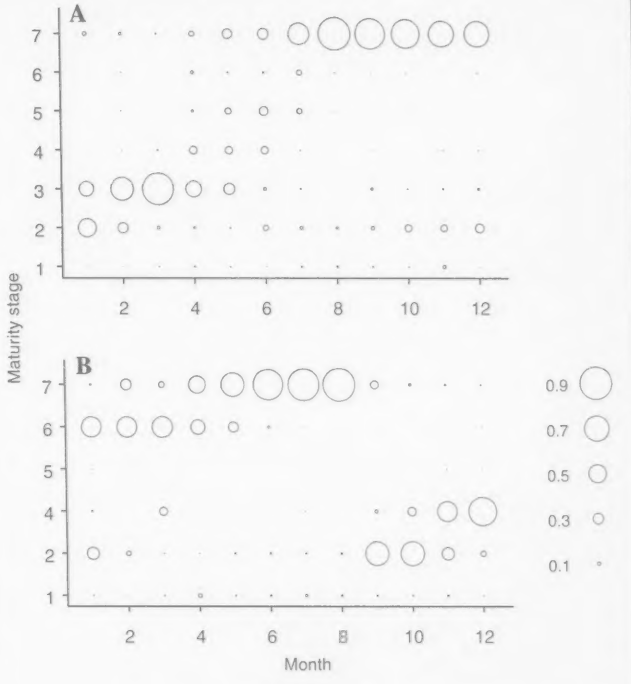

Figure 4

The proportion of each maturity stage within each month for (**A**) female and (**B**) male silvergray rockfish (*Sebastes brevispinis*) (see Table 1 for definition of stages represented by the numbers on the *y* axis).

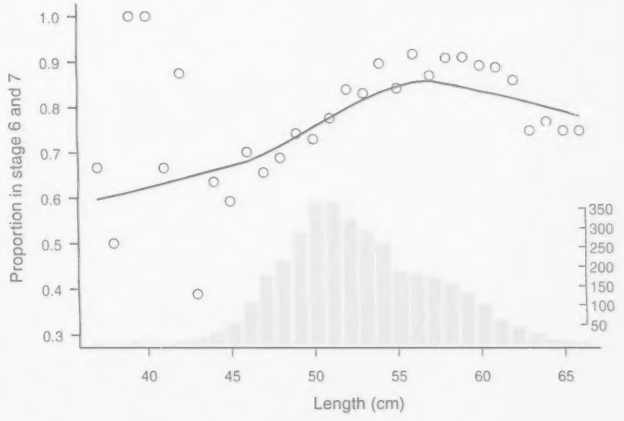

Figure 5

The proportion of all mature (stages 3–7, see Table 1) female silvergray rockfish (*Sebastes brevispinis*) in July samples that were classified as spent or resting (stages 6–7) against length. The number of observations is shown in the histogram.

Table 5

Summary of the predicted values of life history parameters at age for silvergray rockfish (NA: not applicable), partial recruitment values from Stanley and Kronlund (2000).

	Both sexes	Females				Males		
Age (years)	Partial recruitment	Length (cm)	Weight (g)	% mature	Fecundity (10^6)	Length (cm)	Weight (g)	% mature
1	0.000	NA	NA	0.000	NA	NA	NA	0.000
2	0.000	NA	NA	0.000	NA	NA	NA	0.000
3	0.000	NA	NA	0.010	NA	NA	NA	0.000
4	0.000	NA	NA	0.020	NA	NA	NA	0.000
5	0.000	NA	NA	0.041	NA	NA	NA	0.000
6	0.000	NA	NA	0.080	NA	NA	NA	0.103
7	0.000	NA	NA	0.143	NA	NA	NA	0.195
8	0.000	42.680	1158	0.235	NA	42.386	1138	0.330
9	0.000	44.750	1233	0.352	NA	43.348	1205	0.492
10	0.002	45.698	1307	0.479	NA	44.245	1270	0.647
11	0.151	46.593	1379	0.599	NA	45.080	1332	0.770
12	0.283	47.437	1448	0.700	0.496	45.858	1391	0.855
13	0.401	48.233	1516	0.776	0.536	46.583	1448	0.909
14	0.505	48.985	1582	0.833	0.576	47.258	1502	0.942
15	0.596	49.694	1645	0.875	0.616	47.887	1553	0.961
16	0.674	50.363	1707	0.906	0.656	48.473	1602	0.974
17	0.742	50.994	1766	0.928	0.696	49.019	1648	0.982
18	0.799	51.590	1823	0.944	0.736	49.528	1692	0.988
19	0.847	52.152	1877	0.955	0.776	50.002	1734	0.992
20	0.887	52.682	1930	0.962	0.817	50.444	1773	0.995
21	0.919	53.183	1980	0.968	0.857	50.855	1810	1.000
22	0.944	53.655	2029	0.971	0.898	51.238	1845	1.000
23	0.963	54.101	2075	0.967	0.939	51.595	1878	1.000
24	0.977	54.521	2119	0.962	0.981	51.928	1909	1.000
25	0.987	54.917	2161	0.953	1.022	52.238	1938	1.000
26	0.994	55.292	2201	0.949	1.057	52.527	1965	1.000
27	0.999	55.645	2240	0.960	1.087	52.796	1991	1.000
28	0.999	55.978	2276	0.972	1.117	53.046	2015	1.000
29	1.000	56.292	2311	0.985	1.145	53.280	2038	1.000
30	1.000	56.589	2345	0.992	1.166	53.497	2059	1.000
40	1.000	58.774	2598	1.000	1.252	55.002	2210	1.000
50	1.000	59.996	2747	1.000	1.228	55.743	2287	1.000
60	1.000	60.680	2832	1.000	1.069	56.108	2325	1.000
70	1.000	61.030	2881	1.000	NA	56.288	2344	1.000

relationship of silvergray rockfish to other rockfish species was examined by Gharrett et al. (2001).

Growth

Silvergray rockfish age estimates have not been validated as they have been for other rockfish (Bennett et al., 1982; Culver, 1987; Leaman and Nagtegaal, 1987; Andrews et al. 2002; Kerr et al. 2004); however, there is evidence of a modal progression in the year classes (Stanley and Kronlund, 2000).

Our estimated growth rates were similar to those reported by Archibald et al. (1981), who used a small subset of the current data. The maximum recorded size of 73 cm for silvergray rockfish is larger than that for most rockfish but smaller than that reported for the largest rockfishes, such as yelloweye rockfish (*S. ruberrimus*), cowcod (*S. levis*), shortraker (*S. borealis*), and bocaccio (*S. paucispinis*), all of which can exceed 91 cm (Haldorson and Love, 1991). The growth rate of silvergray rockfish is similar to that of other rockfishes (Haldorson and Love, 1991), and weight at length was

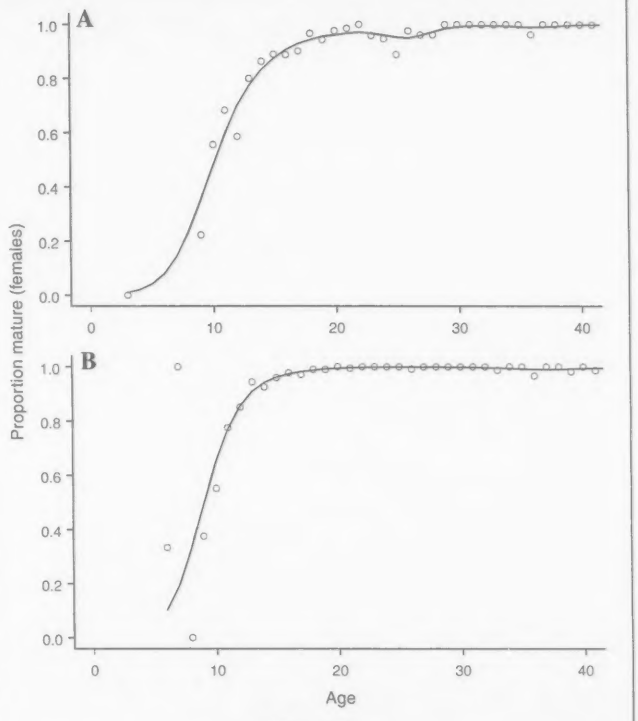

Figure 6

The estimated proportion mature at age for (**A**) female and (**B**) male silvergray rockfish *(Sebastes brevispinis)*.

similar between sexes as is common for most rockfishes (Love et al., 1990).

Lenarz and Wylie Echeverria's (1991) examination of growth dimorphism led them to categorize rockfish as demersal versus water column, and shallow (≤125 m) versus deepwater species (>125 m). Table 4 shows that silvergray rockfish are consistent with other demersal rockfish in that they show relatively little sexual dimorphism in growth. Lenarz and Wylie Echeverria (1991) suggested that the size dimorphism may result from trade-offs between fecundity and size; they suggest that among water-column species, males may optimize size solely for survival, whereas added size for a female may confer advantages in egg production.

Seasonal maturation and age at maturity

The difficulties in the macroscopic staging of rockfish maturity have been widely discussed (Gunderson et al., 1980; Love and Westphal, 1981; Wyllie Echeverria, 1987; Love et al., 1990; Nichol and Pikitch, 1994). These authors are consistent in suggesting that maturity stages should be verified by histological examination of samples collected through all seasons.

More problematic than the staging is the possibility that commercial fishery samples may not be representative of the overall population. If only the mature fraction of an age class recruits to the fishery, then age at maturity derived from commercial samples will underestimate actual age at maturity. For the trawl nets used in the rockfish fishery in British Columbia, size at 100% retention for rockfish is about 30 cm. Silvergray rockfish do not begin to recruit to the fishery until about 35 cm; thus age or size at recruitment is conditioned by behavior of the silvergray rockfish and not by mesh size.

Given the discussion above, our conclusions on age and length at maturity should be viewed as tentative. Nevertheless, the available observations indicate that most females are mature by age nine and most males by age nine or ten. Lenarz and Wylie Echeverria (1991) noted that in 21 of 31 rockfish species, females and males matured at similar ages.

Mating appears to take place from September through January and peaks from December through January. This time range differs from the range derived from observations for southeastern Alaska where ripe male silvergray rockfish were observed from January to March

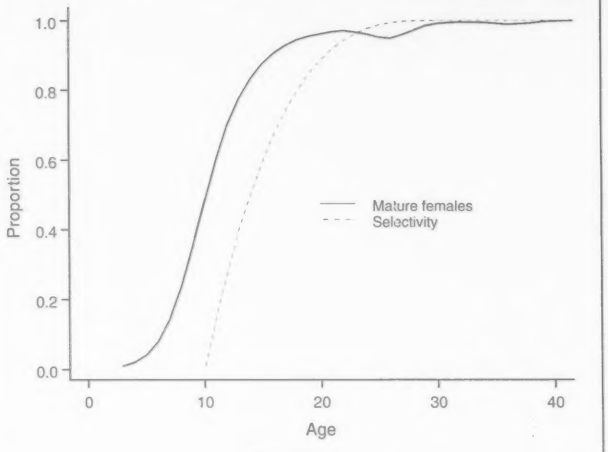

Figure 7

Maturity at age for female silvergray rockfish *(Sebastes brevispinis)* in comparison with estimated age at recruitment.

(O'Connell[8]). Significant proportions of females with fertilized eggs began to appear 2–3 months later in March and peaked from April to May. This lag time does not differ noticeably from that for other rockfish. Wyllie Echeverria (1987) reported that fertilized eggs are usually found 1–3 months after mating. A few specimens with eyed larvae have been observed in February and March but significant proportions are not observed until April. Parturition lasts through July and peaks in June. Westrheim (1975) suggested that the principal month of parturition was later than June for Oregon–B.C. waters, and later than May for the Gulf of Alaska. Phillips (1964) suggested that the timing of rockfish reproduction could be classified into two broad seasons: early (winter) or late (spring–summer). Silvergray rockfish clearly fall within the latter category.

A mating period from December to January and parturition in June implies a 5–6 month process. This is longer than the average period reported for rockfish by Wyllie Echeverria (1987) but similar to those reported for greenstripe rockfish (*S. elongatus*) (Dec–Feb to June), redstripe rockfish (Nov–Jan to June) and sharpchin rockfish (*S. zacentrus*) (Oct–Jan to Apr–May) (Shaw, 1999). The longer periods may reflect that these species and samples were from higher latitudes than the California observations prevalent in Wyllie Echeverria's work. However, Shaw (1999) pointed out that rosethorn rockfish (*S. helvomaculatus*) samples from the same latitudes indicated a maturation process of 1–2 months. Batch spawning has been reported by Moser (1967a, 1967b) for some rockfish species but our histological examination of 11 specimens taken from the April sample provided no indication of this in silvergray rockfish. Samples taken closer to parturition would be more conclusive.

The July samples indicated a dome-shaped relationship in the timing of parturition. As reported for dark-blotched rockfish (Nichol and Pikitch, 1994) and yellowtail rockfish (Eldridge et al., 1991), we observed that the smaller females tended to complete parturition later. However, unlike the results from previous studies, our results indicates that the largest females also tended to complete parturition later.

Fecundity

Different authors have emphasized that actual fecundity at parturition may be lower than estimates derived prior to fertilization (MacGregor, 1970; Boehlert et al., 1982; Haldorson and Love, 1991; Gunderson, 1997), although this was not observed in yellowtail rockfish (Eldridge et al. 1991). Future studies could examine fecundity closer to parturition; however, it is difficult to capture specimens on the verge of parturition without inducing extrusion (Boehlert et al., 1982). We also caution that our estimates are from one sample and Guillemot et al. (1985) reported significant interannual variation in gonadal development among five species of northern California rockfish.

The presence of the *Sarcotaces arcticus* parasite, previously reported for silvergray rockfish (Sekerak, 1975),

[8] O'Connell, V. 1986. Spawning seasons for some *Sebastes* species landed in the Southeast Alaska longline fishery for nearshore rockfishes (1982–1985). Unpublished report, 21 p. Alaska Department of Fish and Game, Division of Commercial Fisheries, 304 Lake St., No. 103, Sitka, AK 99835-7563.

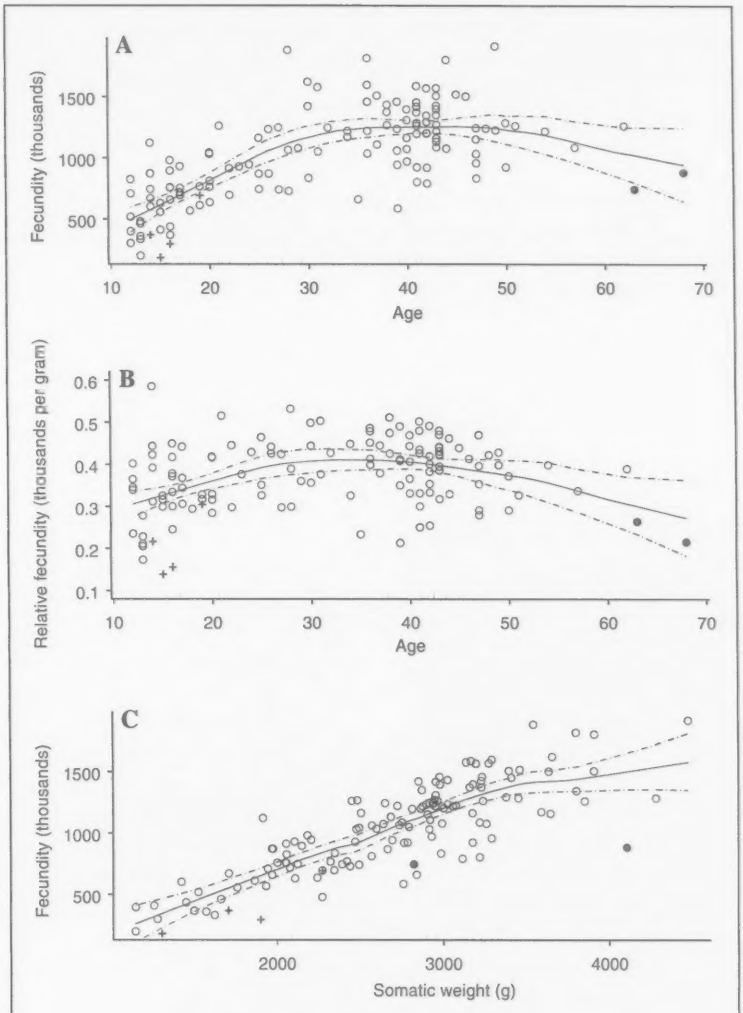

Figure 8

Silvergray rockfish *(Sebastes brevispinis)* fecundity (thousands of eggs) versus (**A**) age, (**B**) relative fecundity (thousands of eggs/g somatic weight) against age, and (**C**) fecundity against somatic weight. Solid circles indicate two possibly anomalous points. The plus symbols indicate females infected by the *Sarcotaces arcticus* parasite. The dashed curves represent the limits of point-wise 95% confidence intervals. The "rug" along the x-axis of each plot shows the frequency of observations of age or size classes.

appears to be associated with reduced fecundity, albeit this conclusion is based on three observations. This conclusion is consistent with qualitative observations by the senior author that the gonads of infected silvergray rockfish tend to be smaller.

Silvergray rockfish fecundity appears typical of the genus as summarized in the meta-data treatment by Haldorson and Love (1991). Predicted fecundity for a 40-year old female exceeds 1,250,000 oocytes, although the maximum observed fecundity in a small sample was almost 2,000,000. The slope of the relationship of log fecundity to log length from our study was 4.283, close to the mean of 4.10 reported for other rockfish (Haldorson and Love, 1991).

Haldorson and Love (1991) noted that the ratio of fecundity at the age of 50% maturity versus fecundity

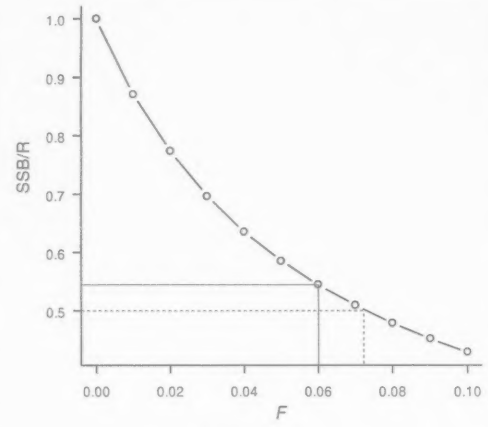

Figure 9

Spawning biomass per recruit (SSB/R) against instantaneous fishing mortality (F) for silvergray rockfish *(Sebastes brevispinis)*.

at the age of maximum fecundity ranged from 0.01 to 0.25 for rockfish. Fecundity at 50% maturity could not be determined because we had no observations for females less than 12 years of age. However, if we use fecundity at age 12 (the youngest fish in our sample) and fecundity at age 40 (the predicted age of maximum fecundity), the ratio exceeds 0.40. This finding supports the contention that age at 50% maturity for silvergray rockfish is less than 12 years and adds credibility to the observation that the age of 50% maturity is lower than the age at 50% selectivity.

Estimates of specific fecundity (fecundity/somatic weight) were 356 and 482 ova/g for the 12-year-old and 40-year-old females, respectively. Given that the age at 50% maturity is probably less than 12 years; this range in "relative investment" in reproduction appears average for rockfish (Haldorson and Love, 1991). As with other rockfish, specific fecundity increases with size, although it appears to reach an asymptote at age 40 for silvergray rockfish.

Age at maturity and SSB/R

An M of 0.06 places silvergray rockfish in the middle to lower end of the mortality range for rockfishes. It is higher than the estimates of 0.02–0.04 reported for yelloweye rockfish (O'Connell and Fujioka[9]; O'Connell et al.[10]; Yamanaka and Lacko, 2001) but much less than 0.14 that has been used for yellowtail rockfish, or 0.28 used for black rockfish (*S. melanops*) (Dorn, 2002).

The analysis of SSB/R indicates that an $F_{50\%}$ corresponds to F=0.072 or F=1.2M. This F to M ratio represents a more aggressive harvest strategy than the range of 0.5–1.0 currently supported in the literature (Patterson, 1992; Walters, 1998). This result is caused by the special case of silvergray rockfish, anticipated by Clark (1991), wherein recruitment at age is delayed in comparison to maturity at age. If most females actually mature by age 11 or 12 years, but are still not 50% vulnerable at age 14 (Fig. 9), then even at a relatively high fishing mortality, most females can reproduce a few times prior to capture.

As stated above, recruitment to the fishery may be driven more by the stage of maturation than by size or age. Movement to areas and depths that are the source for most fishery samples may be governed by behavioral issues associated with maturation. If fish tend to recruit as they become mature, somewhat independent of size or age, then we may underestimate the age of 50% maturity. In this respect, it is interesting that the fecundity data, compared to other rockfish data, also indicate that the age of 50% maturity may be much less than 12 years.

Our suggestion to managers is that unless the nonrecruited population can be sampled to verify maturity-at-age assumptions, then a more precautionary approach is warranted than is implied by an F=1.2M logic for harvest strategy. This silvergray rockfish example emphasizes the sensitivity of an SSB/R harvest logic to estimating age at maturity, which in turns emphasizes the often neglected issues of field classification of maturity and the representativeness of samples. The task of estimating age at maturity is perhaps too often ignored at the expense of estimating other life history parameters.

Conclusion

Owing to the small role that silvergray rockfish has played in groundfish fisheries of the eastern North Pacific Ocean, this species has received little research attention. However, these less valuable stocks are beginning to attract more attention owing to their potential to disrupt precautionary management objectives within the context of a multispecies fishery. With the shift to a more precautionary paradigm, a lack of stock knowledge about the status of any of the incidental species, such as silvergray rockfish, can be a basis for restricting the overall fishery. Strategic allocation of resources by species or stock can no longer be predicated on landed value.

[9] O'Connell, V., C. Brylinsky, and D. Carlile. 1991. Demersal shelf rockfish stock assessment and fishery evaluation report for 2004. Alaska Dep. Fish and Game Regional Information Report J03-39, 44 p. 304 Lake St. #103, Sitka, AK 99835-7563.

[10] O'Connell, V., and J. Fujioka. 1991. Demersal shelf rockfish. *In* Status of living resources off Alaska as assessed in 1991, p. 46–47. NOAA. Tech. Memo. NOAA-TM-NMFS-F/NWC-211. 304 Lake St. #103, Sitka, AK 99835-7563.

Finally, we note how a meta-data analysis such as that provided by Haldorson and Love (1991) can provide values for stock assessment parameters in the absence of direct estimation. By summarizing the basic life history characteristics for silvergray rockfish in B.C. waters, we add to the research on rockfish and improve the basis for effective management of at least one more minor, but potentially fishery-limiting, species in the eastern Pacific groundfish complex.

Acknowledgments

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Appendix 1—Growth formula from Schnute (1981)

$$Y(t)=\left[y_1^b+(y_2^b-y_1^b)\frac{1-e^{-a(t-\tau_1)}}{1-e^{-a(\tau_2-\tau_1)}}\right]^{1/b}.$$

The model involves six parameters, $\Theta=(\tau_1, \tau_2, y_1, y_2, a, b)$, where τ_1 and τ_2 are two arbitrary ages in the life of a fish, such that $\tau_2>\tau_1$. The parameter y_1 is the size of a fish at time τ_1, and y_2 is the size of a fish at time τ_2 with $y_2>y_1>0$. Parameters a and b determine the shape of the growth curve by controlling the acceleration (deceleration) in growth from times τ_1 to τ_2. The parameter a has units (in time), and b is dimensionless. Although the mathematical expression of the model has four cases, these four cases actually represent the limiting forms of a single equation as a or b (or both) approach 0.

Appendix 2—Spawning stock biomass per recruit

If N_a is a vector of the numbers of females at each age under constant conditions, such that

$$N_{a+1}=N_a e^{-(FS_a+M)},$$

where F = the instantaneous fishing mortality rate;
S_a = the partial recruitment at age a; and
M = the instantaneous natural mortality rate;

then the cumulative spawning potential of a cohort of females over the lifetime of the cohort (under constant F and M and S_a) is

$$SSB/R=\sum_1^a N_a Fec_a Mat_a,$$

where Fec_a = fecundity at age a, and
Mat_a = proportion mature at age a.

The spawning potential per recruit (SSB/R) can then be calculated under various estimates of F and compared with the unfished SSB/R (F=0) as shown in Figure 9.

Impact of the California sea lion (*Zalophus californianus*) on salmon fisheries in Monterey Bay, California

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Abstract—To assess the impact of California sea lions (*Zalophus californianus*) on salmon fisheries in the Monterey Bay region of California, the percentages of hooked fish taken by sea lions in commercial and recreational salmon fisheries were estimated from 1997 to 1999. Onboard surveys of sea lion interactions with the commercial and recreational fisheries and dockside interviews with fishermen after their return to port were conducted in the ports of Santa Cruz, Moss Landing, and Monterey. Approximately 1745 hours of onboard and dockside surveys were conducted—924 hours in the commercial fishery and 821 hours in the recreational fishery (commercial passenger fishing vessels [CPFVs] and personal skiffs combined). Adult male California sea lions were responsible for 98.4% of the observed depredations of hooked salmon in the commercial and recreational fisheries in Monterey Bay. Mean annual percentages of hooked salmon taken by sea lions ranged from 8.5% to 28.6% in the commercial fishery, 2.2% to 18.36% in the CPFVs, and 4.0% to 17.5% in the personal skiff fishery. Depredation levels in the commercial and recreational salmon fisheries were greatest in 1998—likely a result of the large El Niño Southern Oscillation (ENSO) event that occurred from 1997 to 1998 that reduced natural prey resources. Commercial fishermen lost an estimated $18,031–$60,570 of gear and $225,833–$498,076 worth of salmon as a result of interactions with sea lions. Approximately 1.4–6.2% of the available salmon population was removed from the system as a result of sea lion interactions with the fishery. Assessing the impact of a growing sea lion population on fisheries stocks is difficult, but may be necessary for effective fisheries management.

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California sea lions (*Zalophus californianus*) interact with almost all commercial and recreational fisheries along the California coast, causing entanglement and damage to fishing gear and loss of catch (Beeson and Hanan[1]; NMFS[2]). The prey of these pinnipeds has been of interest for years because pinnipeds have been viewed as competitors with humans for a variety of fish species. Historically, this competition between pinnipeds and fishermen was of limited importance because fishes and pinnipeds were harvested. However, the increasing specialization within the fishing industry during the twentieth century and changing attitudes toward pinnipeds have intensified this competition (Harwood and Croxall, 1988). Since the passage of the Marine Mammal Protection Act (MMPA) in 1972, the population of California sea lions has increased along the West Coast of North America (NMFS[2]). This increase in pinniped populations has resulted in an increase in the number of reports of pinnipeds interacting with fishing boats and depredating the catch in fisheries along the West Coast (Beeson and Hanan[1]; NMFS[2]).

The California sea lion population, found from offshore islands in Mexico north to Vancouver Island, British Columbia, has increased steadily throughout the latter part of the twentieth century (NMFS[2]). In the early 1900s, the over-riding management philosophy was to limit the California sea lion population because of damage to commercial catches and competition for salmonid fishery resources (Everitt and Beach, 1982). Numbers of sea lions began to increase in the 1940s with curtailment of commercial harvests, but bounties were paid for seals and sea lions in Oregon and Washington until the early 1970s. Following passage of the MMPA in 1972, the California sea lion population increased at an annual average of 5.0–6.2% along the West Coast (Carretta et al.[3]). There are an estimated 204,000–214,000 sea lions in U.S. waters (Carretta et

[1] Beeson, M. J., and D. A. Hanan. 1996. An evaluation of pinniped-fisheries interactions in California. Report to the Pacific States Marine Fisheries Commission, 46 p. Pacific States Marine Fisheries Commission, 205 SE Spokane St., Portland, OR 97202.

[2] NMFS (National Marine Fisheries Service). 1997. Impacts of California sea lions and Pacific harbor seals on salmonids and the coastal ecosystems of Washington, Oregon, and California. NOAA Tech. Memo. NMFS-NWFSC-28, 150 p. Northwest Fisheries Science Center, 2725 Montlake Blvd. East, Seattle, WA 98112-2097.

[3] Carretta, J. V., M. M. Muto, J. Barlow, J. Baker, K. A. Forney, and M. Lowry, editors. 2002. U.S. Pacific Marine Mammal Stock Assessments: 2002. NOAA/NMFS Tech. Memo., NOAA-TM-NMFS-SWFSC-346, 290 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, California 92037-1508.

al.[3]), and an additional 45,000–54,000 animals along Baja, Mexico (Aurioles-Gamboa and Zavala-Gonzalez, 1994). In the Monterey Bay region, sea lions do not breed but several important resting sites exist with a range of 3000 to 7500 animals during the nonbreeding season (Weise, 2000). In contrast to increases in numbers of sea lions, serious declines in salmonid populations have occurred in recent years as a result of changes and degradation in riverine habitat, declines in water quality, overharvesting, changes in oceanic conditions, and the development of hydroelectric power systems that obstruct major riverine migration routes.

Chinook salmon (*Oncorhynchus tshawytscha*) stocks in the Central Valley of California probably represent 85% to 95% of the chinook salmon catches south of Pt. Arena and in Monterey Bay (PFMC[4]). Central Valley chinook originate in the Sacramento River and San Joaquin River and have four distinct runs (portion of a salmon stock that returns to their native streams to spawn during a specific season): fall, late-fall, winter, and spring. Fall and late-fall runs are relatively healthy, but winter and spring runs are listed as endangered under the Endangered Species Act (ESA). Salmon landed in Monterey Bay during the summer fishing season are predominantly fall and late-fall run Central Valley chinook salmon. Size limits and seasonal restrictions are set to reduce retention of listed winter run Central Valley chinook and Klamath River stocks (PFMC[4]). By taking hooked fish, sea lions can affect salmon stocks because commercial and recreational fishermen continue to fish for salmon to replace those taken by sea lion and this activity of predation and compensatory fishing leads to greater numbers of fish being removed from the population. In the ocean commercial troll and recreational salmon fishery, sea lions will swim near or follow fishing boats and will depredate fish once hooked.

Consumption of hooked salmon by sea lions may not only impact salmonid stocks but impact the economic viability of fisheries. Recreational and commercial salmon fishing is an important social and economic asset in California, representing $28,856,000 in revenues in 1995 (PFMC[5]). Concern over declining salmonid stocks has resulted in adjustments of fishing regulations, such as allocation of harvest between ocean and inland user groups, harvest quotas, and time and area closures (Beeson and Hanan[1]). Increasing losses of fish to California sea lions may produce further restrictions for the recreational and commercial salmon fisheries.

[4] PFMC (Pacific Fisheries Management Council). 1999. Review of 1998 ocean salmon fisheries. NOAA Award No. NA97FC0031, sections A1–A50 and B1–43. Pacific Fisheries Management Council, 7700 NE Ambassador Place, Suite 200, Portland, OR 97220-1384.

[5] PFMC (Pacific Fisheries Management Council). 1995. Review of 1994 ocean salmon fisheries. NOAA No. NA57FC0007, sections A1–A50 and B1–B43. Pacific Fisheries Management Council, 7700 NE Ambassador Place, Suite 200, Portland, OR 97220-1384.

During the last several decades only a few researchers have attempted to quantify the impact of sea lions on fisheries in California waters and, more specifically, the Monterey Bay region. According to Beeson and Hanan,[1] the recreational ocean salmon landings in 1995 were greatest in Monterey Bay and San Francisco areas and experienced the greatest amount of sea lion predation (charter passenger fishing vessels and private skiff combined). In our study, we surveyed salmon fisheries in Monterey Bay because of the particularly high rates of interactions with sea lions (Beeson and Hanan[1]) in an effort to better understand the nature and extent of these interactions in the commercial and recreational fisheries.

The purpose of this study was to estimate the percentage of salmon taken by California sea lions from commercial and recreational salmon fisheries in Monterey Bay from 1997 to 1999. We hypothesized that the percentages of fish taken by California sea lions in salmon fisheries would be greater than those taken in previous years and would be part of an increasing trend in sea lion and fisheries interactions paralleling the growth of the sea lion population. Further, we estimated the number of fish removed from the California Central Valley chinook stock from observed percentages of fish taken by sea lions in fisheries. Lastly, we estimated the monetary losses associated with sea lions interacting with commercial and recreational salmon fisheries in Monterey Bay from 1997 to 1999 by quantifying the value of fish lost and the type and amount of gear lost or damaged.

Methods

From 1997 to 1999, observations of interactions between pinnipeds and salmon fisheries were conducted onboard boats, and interviews with fishermen were performed at dockside at the three major ports in the Monterey Bay region: Santa Cruz, Moss Landing, and Monterey (Fig. 1). Salmon fishing operations included commercial troll fishery and recreational fisheries consisting of commercial passenger fishing vessels (CPFVs) and private skiffs. The timing of the commercial and recreational salmon fishery seasons varied each year of the study, and sampling was conducted from the beginning to the end of each season (Table 1). The commercial troll fishery included day boats (i.e., a one-day fishing trip) and multiple-day boats. Fishing areas included in our study ranged from Pt. Sur north to Año Nuevo Island. Data regarding fisheries interactions collected at the three different ports were pooled because fishermen from all three ports often fish as a fleet.

Dockside surveys were conducted to achieve a greater sampling effort than could be obtained from onboard observations alone. Onboard surveys were conducted to test reliability of dockside surveys and to ensure that investigators fully understood the nature of the interaction. Small biases have occurred when combining onboard and dockside surveys but were attributed to

Table 1

Commercial and recreational salmon fishery seasons in the Monterey Bay region from 1997 to 1999.

	Commercial	Recreational
1997	1–31 May, 23 June–18 July, 1–30 September	15 March–19 October
1998	1–31 May, 16 June–30 September	14 March–7 September
1999	1 May – 21 August, 1–30 September	14 March–6 September

onboard sampling in areas where interaction was more prevalent (Miller et al.[6]). During this study, captains were requested during onboard observations to conduct normal fishing operations and not to intentionally seek out areas with greater or lesser rates of interaction between sea lions and fishery operations.

Sampling of commercial and recreational salmon fisheries was stratified by month and approximately equal numbers of onboard and dockside surveys were conducted monthly. Sampling days and ports were selected randomly for onboard and dockside surveys of commercial fishing operations, but onboard surveys were limited by crew cooperation and space availability. Each onboard survey in the commercial fishery took a full fishing day onboard one boat, and dockside interviews were conducted during four-hour periods in the middle to late afternoon during the peak time that vessels returned to port. For CPFVs, which operate virtually every day but have a greater number of boats and passengers on weekends, two-thirds of onboard and dockside sampling dates were selected randomly from possible weekend dates and one-third from all possible weekdays. Onboard surveys of CPFV took a full fishing day aboard one vessel, and dockside surveys took two to three hour periods in early afternoon during peak return times for CPFVs at a randomly selected port. The goal of CPFV dockside surveys was to sample (for the sampling day) all CPFVs targeting salmon and that had returned to port. In the skiff fishery, greater numbers of fishing trips occurred on weekends; therefore approximately three-quarters of sampling days occurred on weekends, and one-quarter occurred on weekdays. Onboard surveys in 1997 aboard one skiff took a full fishing day, and dockside surveys from 1997 to 1999 were conducted during two-hour sampling periods in late morning and early afternoon during the peak return time for private skiffs.

In 1997, four onboard surveys were conducted in the commercial and CPFV fishery, and five onboard private skiff surveys were conducted. Whereas in 1998 and 1999, in an effort to increase onboard sample size, survey effort was concentrated in the commercial and CPFV fisheries; 22 surveys conducted each year in each fishery.

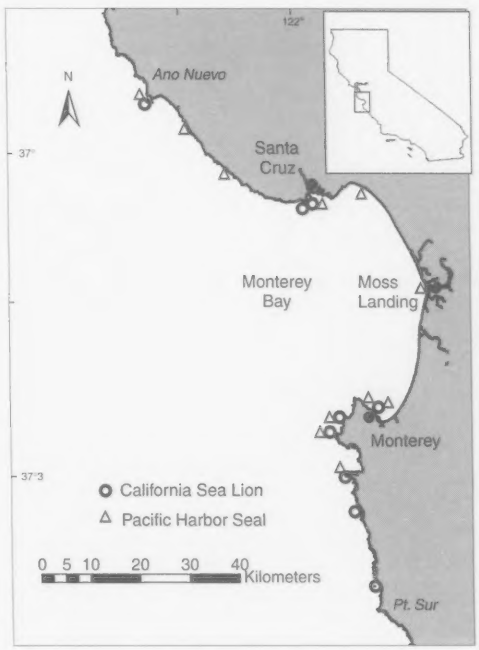

Figure 1

Primary fishing ports used by commercial and recreational salmon vessels, and pinniped haul-out sites in Monterey Bay, California.

Information collected at dockside included port of call, number of fish landed, number of fish taken by pinnipeds at or below the surface, species and number of marine mammals involved in surface take, number of fish released, number of released fish taken by marine mammals, and type and amount of gear loss. Onboard surveys included the same information collected at dockside, as well as standard length of all fish landed.

Commercial troll and recreational salmon fisheries use different types of fishing gear, which can affect the nature and magnitude of their interactions with pinnipeds. Commercial salmon trolls are designed to catch fast-swimming fishes by using flashy lures that are trolled behind the moving vessel on heavily

[6] Miller, D. J., M. J. Herder, and J. P. Scholl. 1983. California marine mammal-fishery interaction study, 1979-1981. NMFS Southwest Fish. Cent., Admin. Rep. LJ-83-13C, 233 p. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508.

weighted fishing lines. Multiple lines are mounted on outrigger poles to ensure separation of the lines and are controlled by small hydraulic winches (Starr et al., 1998). Depending on conditions, commercial fishermen use three to fifteen lures per line and two to six lines per boat, totaling six to ninety lures with hooks per boat. In recreational boats each fisherman traditionally uses one rod, reel, line, and hook with bait.

Surface takes, also termed "definite takes," were defined as takes when pinnipeds took a hooked salmon (and when the species and number of marine mammals involved could be determined). Surface takes were also recorded when fish were hooked and the action of the line indicated that a fish was no longer hooked, and a pinniped surfaced immediately with a fish in its mouth. Takes below the surface, or "probable takes," were defined as takes when fish were removed from the hook (and when the species and number of marine mammals involved could not observed directly). Evidence that indicated the occurrence of below-surface takes was in the form of bent hooks, lost gear, or a sea lion surfacing within several minutes with a salmon, provided no other fishing boats were in close proximity. Two types of takes were designated because takes below surface were not witnessed, and other predators including sharks take fish from lines, or fish may have escaped. However, fishermen and researchers recognized that takes by pinnipeds, specifically by sea lions, differed from takes by sharks and other predators by the action of the line, effect on the hook or lure (or both), and type of bite on fish parts remaining on the hook.

Number of salmon and percentage of catch taken by pinnipeds were compared with the total catch and the legal catch in commercial and recreational fisheries. Total catch was defined as numbers of fish hooked, including all legal-size fish, fish taken by pinnipeds, and all undersize fish. Legal catch represented only fish of legal size landed by anglers. Our rationale for using total catch was that all fish, regardless of size, have an equal probability of being taken by pinnipeds; therefore, comparisons with total catch were a more accurate metric for quantifying the impact of pinnipeds on the salmon fishery. Comparisons with the legal catch inflated the percentage of fish taken by pinnipeds and exacerbated the perception of the problem of pinnipeds interacting with salmon fisheries. However, previous researchers have compared percentage takes by pinnipeds with legal catch; therefore we also made the comparison with legal catch to place our results in a historical context.

Mean percentages of fish taken by sea lions in relation to total catch (referred to as "mean percentage of fish taken by sea lions") for the commercial, CPFV, and skiff fisheries for onboard and dockside surveys from 1997 to 1999 were non-normal in distribution and were transformed by using the arcsine transformation for parametric statistical comparisons (Zar, 1996). Mean percentages of fish taken by sea lions in the three fisheries (commercial, CPFV, and skiff) were compared between onboard and dockside surveys, among years (1997 to 1999), between seasons (sea lion breeding and nonbreeding seasons), and between takes (surface and below surface) using a Students t-test and ANOVA or a Mann-Whitney U-test and Kruskal-Wallis test for data that were non-normal and heteroscedastic after transformation.

Sea lion breeding and nonbreeding seasons from 1997 to 1999 were determined by using aerial and ground counts from Weise (2000). The breeding season was designated as the time when a significant decline in the number of breeding adult males was recorded at haul-out sites in the Monterey Bay region, when animals where presumably heading for the breeding rookeries in southern California. Typically the breeding season is from June and July, and the nonbreeding season occurs during the months of March, April, May, August, and September.

Mean catch per unit of effort, or the numbers of fish hooked per day per boat, in commercial, CPFV, and skiff fisheries data were non-normal and heteroscedastic, therefore, were they were transformed by using $\sqrt{count}+1$ (Harvey, 1987; Zar, 1996). Mean catch per unit of effort for the three fisheries was compared among years with an ANOVA.

To estimate the impact of California sea lion depredation on salmon populations in Monterey Bay we compared estimated numbers of hooked salmon taken by sea lions and the Central California Valley index (CVI) for chinook salmon abundance. The CVI is the numbers of ocean- and inland-harvested Chinook salmon and the sum of all runs of chinook on the Sacramento Rivers (PFMC[4]) and represents presumably the population of salmon passing through the Monterey Bay region during the fishery season. The estimated number of salmon taken was calculated from the observed number of takes in the commercial and recreational fishery multiplied by the percentage of the total catch that was sampled. Percentage of the total catch sampled was estimated by dividing the number of observed legal-size fish landed by the total number of legal-size fish landed (CDF&G, unpubl. data[7]).

Monetary losses resulting from sea lion interactions with salmon fisheries were estimated by evaluating numbers of fish taken by sea lions and types and quantities of fishing gear damaged or lost during these interactions. Information for the analysis of monetary loses was collected during dockside and onboard surveys for commercial and recreational salmon fisheries.

Annual monetary losses resulting from fish taken by sea lions were calculated by using total numbers of estimated takes by sea lions, average dressed mass (mass of gutted and cleaned fish) of salmon landed in Monterey from 1997 to 1999, and average exvessel price (wholesale price per pound of fish paid to fishermen) for chinook salmon in California from 1997 to 1999 (PFMC[4]). Estimated numbers of takes by sea lions in Monterey Bay from 1997 to 1999 were a function of

[7] CDF&G (California Department of Fish and Game). 2004. Ocean Salmon Project database. CDF&G Ocean Salmon Project, 475 Aviation Blvd., Suite 130, Santa Rosa, CA 95403.

numbers of observed takes (based on dockside samples) and proportions of the total catch sampled.

Estimates of lost and damaged gear were calculated by using average costs for each type of gear used in commercial and recreational salmon fishing operations. A survey of the seven local retail fishing tackle stores in Santa Cruz, Moss Landing, and Monterey was used to estimate mean value of each type of fishing gear used in the recreational (CPFV and skiff combined) salmon fishery. All charter-fishing companies in the three ports in Monterey Bay were surveyed to estimate mean cost of a "setup" sold by charter boat companies to customers. A "setup" was defined as a hook and leader, or a hook, leader, and a 4 oz. or 8 oz. lead sinker. Costs of commercial fishing gear were estimated by surveying 19 local fishermen from the three ports in Monterey Bay. Commercial fishermen buy the majority of their gear in bulk, and often by mail order to reduce costs.

Results

From 1997 to 1999, 1745 hours of onboard surveys and dockside interviews were conducted in the commercial and recreational salmon fisheries. In 1997, 337 hours of onboard and dockside surveys were conducted, 144 hours in the commercial fishery, 103 hours in the CPFV fishery, and 90 hours in the skiff fishery. In 1998, 704 hours of onboard and dockside surveys were conducted: 370 hours in the commercial fishery, 270 hours in the CPFV fishery, and 64 hours in the skiff fishery. During 1999, 704 hours of onboard and dockside surveys were conducted, 410 hours in the commercial fishery, 258 hours in the CPFV fishery, and 36 hours in the skiff fishery. Increased sampling effort in 1998 and 1999 were the result of increased onboard survey effort in the commercial and CPFV fisheries.

During this study 101 onboard surveys and 2780 dockside interviews (number of boats sampled) were conducted in the commercial and recreational salmon fisheries. There were no significant differences in mean percentages of fish taken by sea lions between onboard and dockside surveys in the commercial (1997, P=0.329; 1998, P=0.623; 1999, P=0.653), CPFV (1997, P=0.276; 1998, P=0.660; 1999, P=0.327) and skiff fisheries (1997, P=0.052; Fig. 2). We assumed, therefore, that dockside surveys provided a representative measure of pinniped takes in the salmon fisheries and onboard survey data were pooled with dockside interview data for subsequent analysis.

A total of 967 interviews with commercial fishermen and 1813 interviews with recreational fishermen were were conducted at dockside in Monterey Bay, accounting for 41,895 and 15,115 hooked salmon, respectively (Table 2). In the commercial fishery a similar number of interviews were conducted in 1997 and 1998, whereas in 1999 approximately 21.2% greater numbers of interviews were conducted with the same effort. However, the number of fish landed in 1999 was significantly less than in 1997 and 1998. In the CPFV fishery, the trend

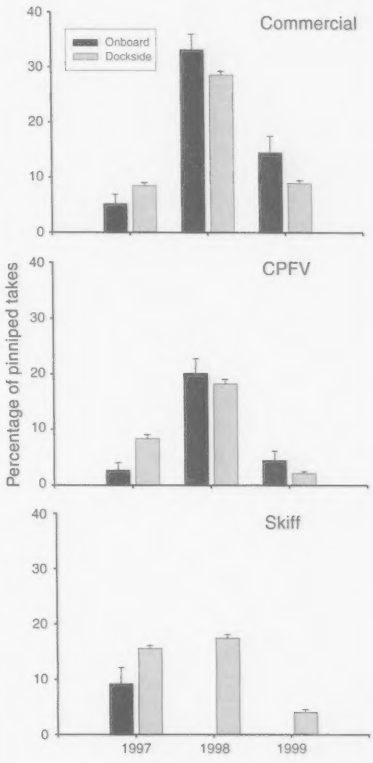

Figure 2

Percentage of pinniped takes in relation to the total number of salmon hooked as determined from dockside and onboard surveys for the commercial, commercial passenger fishing vessel (CPFV), and personal skiff fisheries in Monterey Bay, California, from 1997 to 1999. Onboard survey effort concentrated in CPFV and commercial fisheries during 1998 and 1999. Error bars indicate one standard error.

was similar to the commercial fishery, but the number of fish landed and the number of boats surveyed was significantly fewer overall. In the skiff fishery, there was a steady decline in the number of fishermen surveyed and the number of fish landed from 1997 to 1999.

Onboard observations combined with dockside interviews revealed that California sea lions were almost exclusively responsible for the depredation of hooked salmon in the commercial and recreational fisheries in Monterey Bay, taking 98.4% of the 1199 observed hooked salmon from 1997 to 1999. Of the estimated 2420 takes in 1997, 1072 were directly observed surface takes and sea lions were identified in 98.6% of the takes (Table 2). In 1998, approximately 501 of 5542 takes

Table 2

Yearly catch statistics and estimates of the number and percentage of salmon taken by pinnipeds in the commercial, commercial passenger fishing vessel (CPFV), and skiff salmon fisheries during dockside surveys in Monterey Bay in 1997, 1998, and 1999.

			Catch statistics			Number of takes		Percentage of takes	
Fishery	Year	Number dockside interviews	Total number of fish hooked	Number of legal-size fish landed	Number of under-size fish	Number of fish taken at surface	Number of fish taken below surface	Total % of legal catch lost	Total % of total catch lost
Commercial	1997	297	17,943	12,288	4124	522	1009	12.5	8.5
	1998	293	15,446	6206	4829	97	4314	71.1	28.6
	1999	377	8506	6785	966	37	718	11.1	8.9
	Total	967	41,895	25,279	9919	656	6041	26.5	16.0
CPFV	1997	139	5168	3157	1577	247	187	13.7	8.4
	1998	179	4694	3267	569	305	553	26.3	18.3
	1999	58	362	319	35	6	2	2.5	2.2
	Total	376	10,224	6743	2181	558	742	19.3	12.7
Skiff	1997	723	2926	1643	828	303	152	27.7	15.6
	1998	538	1564	882	409	99	174	31.0	17.5
	1999	176	401	315	70	8	8	5.1	4.0
	Total	1437	4891	2840	1307	410	334	26.2	15.2

occurred at the surface, and sea lions were identified in 98.4% of those takes. In 1999, 51 of the 779 takes occurred at the surface, and sea lions were responsible for 96.1% of the takes. We assumed sea lions took similar percentages of fish below the surface. As evidence of takes below the surface, sea lions would come to the surface within minutes with a fish. Pacific harbor seal (*Phoca vitulina richardsi*) was responsible for other observed takes.

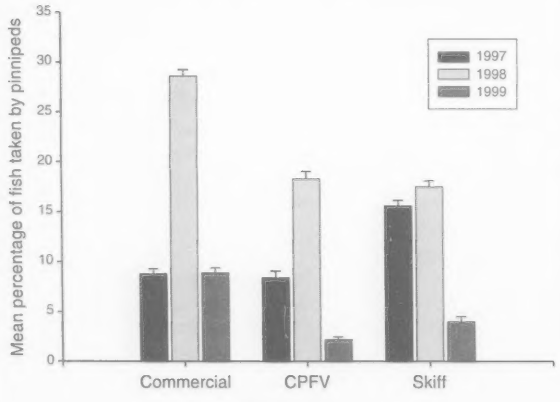

Figure 3

Mean percentage of salmon taken by California sea lion (*Zalophus californianus*) as determined from onboard and dockside surveys of the commercial, commercial passenger fishing vessel, and skiff fisheries in Monterey Bay, California, from 1997 to 1999. Error bars indicate one standard error.

Percentages of the catch taken by sea lions, based on pooled dockside and onboard surveys, were significantly different among years in the commercial ($P<0.000$), CPFV ($P<0.000$), and skiff fishery ($P<0.000$; Fig. 3). During 1998, significantly greater percentages of salmon were taken in the commercial (Tukey HSD multiple comparison, $P<0.000$), CPFV (Tukey HSD multiple comparison, $P<0.000$), and skiff fisheries (Tukey HSD multiple comparison, $P<0.000$). Whereas during 1999, the CPFV (Tukey HSD multiple comparison, $P<0.000$) and skiff fisheries (Tukey HSD multiple comparison, $P<0.000$) experienced significantly smaller percentages of sea lion takes. In the commercial fishery there was no difference in the percentage of fish taken between 1997 and 1999.

Although the timing of the sea lion migration varied by year (Weise, 2000), the percentages of takes by sea lions were greater during the nonbreeding season than during the breeding season in all three years (Fig. 4). In the commercial fishery, those differences were significant for all three years (1997, $P<0.000$; 1998, $P=0.001$; 1999, $P=0.041$). In the CPFV fishery, significantly more takes occurred during the nonbreeding season in 1997 ($P=0.010$), and 1998 ($P<0.000$); however, there was no significant difference in 1999 ($P=0.358$). In the skiff fishery, significantly more takes by sea lions occurred during the non-

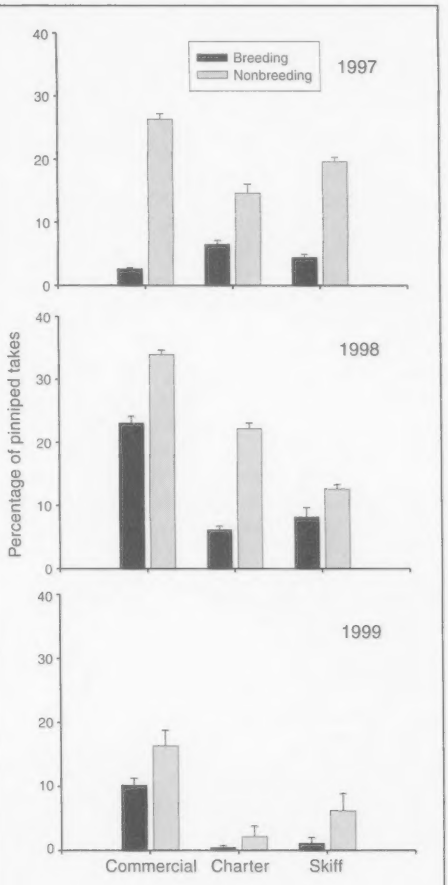

Figure 4

Mean percentage of fish taken by pinnipeds during the California sea lion (*Zalophus californianus*) breeding and nonbreeding seasons in the commercial, commercial passenger fishing vessel (CPFV), and personal skiff fisheries in Monterey Bay, California, from 1997 to 1999. Error bars indicate one standard error.

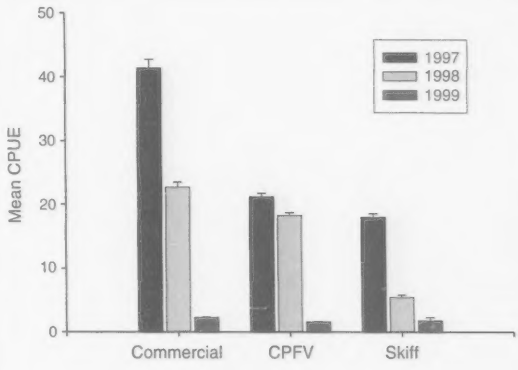

Figure 5

Mean catch per unit of effort (mean number of fish caught per day) in commercial, commercial passenger fishing vessel (CPFV), and skiff fisheries in Monterey Bay, California, from 1997 to 1999. Error bars indicate one standard error.

breeding season of 1997 ($P<0.000$), whereas in 1998 ($P=0.158$) and 1999 ($P=0.358$) there was no significant difference. During all three years, surveys were conducted on commercial, CPFV, and skiff fisheries during August and September; however, there was little to no salmon fishing effort because of the perceived sea lion problem and because the remaining fishermen targeted albacore tuna or rockfishes (or both).

Because of the different styles of hook-and-line fishing in the commercial troll and recreational salmon fisheries, sea lions were more likely to take fish below the surface from commercial trollers but to take fish at and below the surface from recreational vessels. In the commercial fishery, according to dockside interviews and onboard surveys combined, percentages of takes by sea lions below the surface of the water varied throughout the season and were significantly greater than surface takes in 1997 ($P=0.001$), 1998 ($P<0.000$), and 1999 ($P<0.000$; Table 2). In contrast, in the recreational fishery the percentages of takes by sea lions below the water's surface and at the surface varied by year. During 1997, greater percentages of takes by sea lions occurred at the surface than below the surface on CPFVs ($P=0.082$) and skiffs ($P=0.001$; Table 2). Whereas in 1998, significantly greater percentages of takes occurred below the surface in the CPFV ($P<0.000$) and skiff fisheries ($P<0.000$; Table 2). And in 1999, no differences between surface and below surface takes were detected for CPFV ($P<0.972$) or skiff fisheries ($P<0.310$); however this lack of significance was likely due to small sample sizes.

The catch per unit of effort (CPUE: number of fish landed per boat per day) was significantly less in 1998 than in 1997 for the commercial ($P<0.000$), CPFV ($P=0.011$), and skiff fisheries ($P<0.000$) in Monterey Bay (Fig. 5). In 1999, significantly fewer fish were caught than in 1998 and 1997 in the commercial ($P<0.000$) and CPFV ($P<0.000$) fisheries; however, there was no significant difference in the skiff fishery. The percentage of the CVI abundance for chinook salmon taken by sea lions from 1997 to 1999 ranged from 1.4% to 6.2% (Table 3).

From 1997 to 1999, commercial fishermen lost an estimated \$22,333–\$60,077 of gear, and \$224,011–\$504,548 worth of fish as a result of interactions with sea lions (Table 4). The recreational fisheries lost between \$172 and \$18,533 worth of gear as a result of sea lion interactions from 1997 to 1999. Estimates of gear and fish loss were extrapolated from observed losses to total losses based on percentages of the fisheries that were sampled. Gear types varied among commercial

Table 3

Estimates of the pinniped predation index derived from estimates of observed takes of salmon by sea lions (*Zalophus californianus*) in Monterey Bay in relation to the California Central Valley chinook abundance index from 1997 to 1999. Data for Central Valley chinook abundance index were obtained from Pacific Fisheries Management Council, 1999.

	Estimated pinniped takes				
Year	Commercial	Recreational	Total	Central Valley chinook abundance index (Ocean + river totals)	Pinniped predation index (%)
1997	24,258	14,576	24,258	1,055,300	2.2
1998	40,585	9868	40,585	611,800	6.2
1999	8780	269	8780	636,500	1.4

Table 4

Estimates of monetary impact of California sea lion interactions with commercial and recreational salmon fisheries resulting in gear and fish loss in Monterey Bay from 1997 to 1999. Recreational fishery includes commercial passenger fishing vessels and private skiffs. Value of commercial fishery revenues were obtained from the California Department of Fish and Game ocean salmon database. n/a=not applicable.

Fishery	Year	Percentage fishery sampled	Value of gear loss	Value of fish loss	Commercial revenues	Equivalent percentage of commercial revenue lost
Commercial	1997	6.3	$51,609	$375,470	$2,651,499	14.2
	1998	10.9	$60,077	$504,548	$598,062	84.4
	1999	8.6	$22,333	$224,011	$874,100	25.6
Recreational	1997	6.1	$18,533	n/a	n/a	n/a
	1998	11.5	$16,485	n/a	n/a	n/a
	1999	8.9	$172	n/a	n/a	n/a

and recreational fisheries, and gear cost for each fishery varied greatly; therefore, an average estimate for each gear type was used to estimate gear loss for commercial and recreational fisheries. Total revenue losses as a result of fish taken by sea lions in the commercial fishery were equivalent to between 14.2% and 84.4% of the total salmon fishery revenues.

Discussion

Conflicts between pinnipeds and fisheries are well documented in California (Briggs and Davis, 1972; Fiscus, 1979; Ainley et al., 1982; Miller et al.[6]; Hanan et al., 1989; Beeson and Hanan[1]; NMFS[2]). California sea lions have been the primary pinniped species involved in taking fish in ocean commercial and recreational salmon fisheries (Miller et al.[6]; Hanan et al., 1989; Beeson and Hanan[1]). In comparing present results and past studies it is imperative to distinguish between the percentage of salmon taken by pinnipeds relative to the number of legal size fish landed (i.e. legal catch) and number of pinniped takes relative to total number of fish hooked (i.e., total catch). The former value inflates percentages by not including undersize fish caught, whereas the latter includes all fish hooked in the calculation and assumes all fish, regardless of size, have an equal probability of being taken by sea lions.

Dockside surveys were representative of the magnitude of interactions between sea lions and salmon fisheries because there were no significant differences in mean percentages of takes by sea lions between onboard and dockside surveys. Onboard surveys alone would not provide sufficient samples to adequately assess levels of interactions between sea lions and salmon fisheries; conversely, the validity of dockside surveys alone would be questionable because of biases associated with dockside surveys. Biases included fishermen not providing truthful information, fishermen avoiding the survey, fishermen not answering all questions, and not all fishermen returning to the docks. Combining onboard and dockside surveys enabled us to verify dockside findings, obtain sufficient levels of sampling for comparisons, and directly observe and understand the nature of the interactions.

The percentage of hooked salmon taken by sea lions in the commercial salmon fishery in relation to the legal catch has increased by at least 8% since the 1970s and 1980s. Briggs and Davis (1972) reported that California sea lions took 4.1% of all salmon hooked during the

1969 commercial and sport salmon season, Miller et al.[6] reported that in 1981 sea lions took 3.0% of the legal catch during commercial salmon activities, and Beeson and Hanan[1] found that sea lions took 15% of the legal catch in commercial fisheries in 1995. In Monterey Bay in 1997, 12.5% of the legal catch was taken by sea lions, 71.1% in 1998, and 11.1 % in 1999.

Predation levels in the CPFV fishery have increased by at least 8% since 1983, and approximately 3% since 1995. Miller et al.[6] reported predation rates of 5.2 % for the CPFV legal catch in Monterey Bay, and Beeson and Hanan[1] reported predation rates of 10.5 % of the legal catch for the recreational fishery in 1995 (CPFV and private skiff combined). In Monterey Bay, 13.7 % of the legal catch was taken by sea lions in 1997, 26.3 % in 1998, and 2.5 % in 1999.

In the skiff portion of the recreational salmon fishery, predation of the legal catch has increased by at least 26% since 1983, and 17% since 1995. Miller et al.[6] reported predation levels of 1.4% on the legal catch for skiff fisheries in Monterey Bay, and Beeson and Hanan[1] reported predation levels of 10.5% on the legal catch for the 1995 recreational fishery season (CPFV and private skiff combined). In Monterey Bay, predation on the legal catch was 27.7% in 1997, 31.0% in 1998, and 5.1% in 1999. Skiff fishermen typically fish in large groups called "the fleet." Sea lions had a greater probability of getting a hooked salmon when there were greater numbers of hooks in the water; therefore, sea lions most likely target a fleet of fishing boats. Skiff fishermen caught fewer fish than did commercial or CPFV fishermen, but lost a proportionally greater number of fish to sea lions.

The greatest levels of sea lion predation in commercial and recreational fisheries occurred in spring when the greatest numbers of adult male sea lions were migrating south to breeding rookeries in southern California and Baja California, Mexico. In 1997 and 1999, predation levels dropped significantly in June and July following a high level in May, corresponding to declines in numbers of sea lions in Monterey Bay as males headed southward to breeding colonies (Weise, 2000). In 1998, loss of catch to sea lions was greatest in May; slight decreases occurred in percentages of fish taken during June and July because the decline in numbers of adult male sea lions during the breeding season was far less and shorter in duration than in June and July of 1997 and 1999.

We concluded that adult male sea lions took the majority of hooked fish because animals identified taking fish during boat surveys were almost exclusively adult male sea lions and percentages of fish taken by sea lions were less during the sea lion breeding season. Briggs and Davis (1972), Miller et al. [6], and Beeson and Hanan[1] also reported greater numbers of salmon taken in spring (the nonbreeding season) in the commercial and recreational salmon fisheries. Loss of catch to sea lions would most likely be greater during the northward migration of male sea lions because greater numbers of animals would be in the Monterey Bay region; however, fishing effort declined sharply and the commercial season was closed during a portion of that period in 1997.

Sea lions took most salmon below the water's surface in the commercial fishery and both at and below the surface in recreational fisheries. Commercial fishermen lost fish below the surface as a result of the large amount of trolling gear used, and the time required for pulling gear when fish were hooked. Commercial fishermen typically need five to 10 minutes, and as long as 20 minutes to pull hooked fish from the water, allowing ample time for sea lions to take fish. Before the 1994 amendments to the MMPA, sea lions were legally killed for endangering commercial catches, gear, and fishermen, and are still at risk for harassment for taking fish off hooks today. Consequently, most fish in the commercial fishery are taken below the surface and consumed at the surface some distance from the boat because of a combination of the time required to bring a fish to the surface and the threat of harassment. Less gear and perhaps different types of gear that can bring a fish to the surface faster may reduce the number of takes below the surface and overall predation levels. In recreational fisheries, fishermen typically used rod and reel, which allowed fish to be reeled in within minutes. It has been illegal for recreational fishermen to harass or kill sea lions since the passage of the MMPA in 1972; therefore it is not uncommon to see sea lions swimming next to recreational boats in close pursuit of fish that are pulled from the water or that are taken just before they are netted.

Increased depredation levels in the commercial and recreational salmon fisheries in 1998 were most likely the result of the large El Niño Southern Oscillation (ENSO) event that occurred during 1997–98. The 1997–98 ENSO event created large anomalies in physical and biological conditions in the coastal waters off California resulting in above average seasonal norms in sea surface temperatures and large displacements in the distribution of many fish species (Lynn et al., 1998). A combination of factors during the large ENSO event contributed to increased predation on salmon catches. These factors included shifts in sea lion prey composition, decreases in sea lion prey populations, increases in number of sea lions in the region, decreases in fishing effort by commercial and recreational salmon fishermen, and decreases in number of salmon landed. Intensified depredation of catch has been reported during past ENSO events by commercial gillnet fishermen (Beeson and Hanan[1]).

Increased intensity in depredation of hooked fish by pinnipeds during ENSO events may be indicative of decreased foraging success resulting from shifts in prey availability and abundance. A significant shift in sea lion diet occurred between 1997 and 1998 from market squid, northern anchovy, and Pacific sardine to Pacific sardine and anchovy (Weise, 2000). Concurrently, commercial catches of squid, hake, and herring, common prey of sea lions, were low or virtually nonexistent from the fall of 1997 through the summer of 1998 (CalCOFI,

1999). In May 1998, the catch rate for pelagic-young-of-the-year rockfish was the lowest in the history of tri-annual rockfish surveys (Lynn et al., 1998). It is, therefore, reasonable to assume that sea lions were probably nutritionally stressed by the lack of prey and change in prey species and found a hooked salmon an attractive and easy meal.

Mean numbers of California sea lions recorded during the northward migration in summer and autumn of 1998 were approximately 2000 individuals greater than in the summer and autumn of 1997 and 1999, most likely in response to poor foraging conditions in southern California resulting from ENSO conditions (Weise, 2000). During the 1983 and 1992 ENSO events, numbers of sea lions increased along the central California coast owing to the enhancement of the normal northward migration of sea lions resulting from poor food availability in the Southern California Bight (Sydeman and Allen, 1999). During the 1983–84 ENSO, older juvenile sea lions migrated in greater than usual numbers from southern to central California (Trillmich et al., 1991). Greater numbers of female sea lions were counted on Año Nuevo Island in summer and fall 1998, presumably in response to poor foraging conditions in southern California (Morris, unpubl. data[8]). Increases in numbers of sea lions in Monterey Bay during 1998 were most likely due to increases in numbers of juveniles and adult females that moved northward because of the lack of schooling prey species in southern California resulting from the ENSO.

Presumably as a result of ENSO conditions, total landings of salmon and the catch per unit of effort in commercial and recreational fisheries were significantly less in 1998 than in 1997. During our sampling effort in 1998, approximately 2000 fewer fish were landed in commercial and recreational fisheries than in 1997, although approximately double the percentages of fisheries (total salmon landings) were sampled dockside. Numbers of salmon landed in Monterey Bay in 1998 decreased by 59.6% in the commercial fishery and 49.4% in the recreational fishery (PFMC[4]). In California during 1998, numbers of salmon landed in the commercial fishery were 55.7% less than in 1997, and 46.7% less in the recreational fishery. In 1998, CPUE of the commercial fishery declined proportionally more than in other fisheries, which corresponded to proportionally greater percentages of fish taken by sea lions. In Monterey Bay, numbers of angler trips in 1998 declined by 38.6% in the commercial fishery, and 39.9% in the recreational fishery (PFMC[4]). Therefore, there were fewer boats actively fishing, fewer fish being landed, and greater numbers of sea lions in the area, under these conditions, when a fish was hooked, it was more likely to be depredated.

Conversely, in 1999 the depredation levels in the commercial and recreational salmon fisheries in Monterey Bay were significantly less as a result of cool and highly productive La Niña oceanographic conditions. Following one of the strongest ENSO events on record during 1997–98, there was a dramatic transition to highly productive cool-water La Niña conditions and anomalous, upwelling-favorable, wind forcing along the West Coast (Schwing et al., 2000). Upwelling anomalies off the central California coast during 1999 were the greatest in the 54-year record of the upwelling index (Schwing et al., 2000). Record harvest levels of Pacific sardines (CalCOFI, 2000) and greater frequency of occurrence of sardine in the diet of sea lions in central California during the 1999 La Niña (Weise, 2000) indicated that ample prey fishes were available for foraging California sea lions; therefore, depredation pressure on the salmon fisheries was reduced.

Monterey Bay was selected for the present study because it experienced the greatest levels of depredation during the 1995 commercial and recreational fisheries season (Beeson and Hanan[1]). Although Monterey Bay experienced increased levels of pinniped predation in recreational fisheries in 1997 and commercial and recreational fisheries in 1998, these levels were probably not representative of the whole California coast but were more likely the worst-case scenario. Pinniped depredation may be increasing in other areas along the California coast as the sea lion population increases, but probably not to the degree that was observed in Monterey Bay. Pinniped predation of hooked fish in salmon fisheries is probably spatially and temporally variable. Whereas this variability complicates evaluating pinniped impacts on fisheries, it is important for fishery managers to take this variability into account.

Estimated levels of depredation reported for the commercial and recreational salmon fisheries in Monterey Bay may be affected by many assumptions. Lack of direct validation for information received during dockside surveys had unknown impacts on estimates of predation levels, but concurrent onboard sampling appeared to alleviate this bias. Commercial and private skiff salmon boats bypass the sampling docks when no fish are landed or they dock in a harbor slip. Boats that bypass sampling docks may have no fish because of predation by sea lions, and not sampling these boats would result in underestimates of predation levels, but the magnitude of this decrease was difficult to evaluate. Surveys of fishermen were limited by crew cooperation and therefore, not all fishing styles and locations were sampled. The lack of some data would have an impact on predation levels. Surveys of fishermen also were limited to boats fishing for one day because boats fishing for multiple days often fished outside the study area during the course of a trip; however, boats fishing for multiple days were surveyed at dockside so that any biases of onboard samples would have been detected in comparisons of dockside and onboard predation levels.

Depredation of salmon by California sea lions in Monterey Bay could negatively impact salmon populations along the Central California coast. Pinniped depredation of hooked salmon from the California Central

[8] Morris, P. A. 1999. Abstract. 13th Biennial conference on the biology of marine mammals; Maui, HI, 131 p. The Society for Marine Mammology. http://www.marinemammology.org/

Valley chinook salmon population went from a low of approximately 1.4% during a non-ENSO year to an estimated 6.2% during an ENSO season. High harvest levels coupled with high natural depredation of salmon during an ENSO year could be devastating for the Central Valley Chinook salmon population. Further, when sea lions take fish in the fishery, fishermen continue to fish to replace depredated fish, further impacting the salmon population. Hooked salmon lost to sea lions are losses to the population and need to be considered when determining allotments, quotas, and area closures. To better estimate impacts of sea lion predation on the CVI, concurrent studies of sea lion and salmon fishery interactions and sea lion food habits need to be conducted along the entire Central California coast, including Half Moon Bay, San Francisco Bay, and the Farrallon Islands. Sea lions are only one of many natural predators of commercially important fish species. Identifying other natural predators and assessing their impact on prey populations is difficult but necessary for effective fisheries management.

It is likely that only a small proportion of the sea lion population, particularly adult males, were responsible for salmon taken off hooks in salmon fisheries. Percentages of fish taken off the hook declined in all years when adult males moved south during the breeding season in June and July. However, greater percentages of takes occurred in the fisheries in August and September when lesser numbers of adult male sea lions were present in the region. On any given fishing day peak numbers of sea lions were counted at haul-out sites from late-morning to early afternoon, which is also the period when most fishing occurred (Weise, 2000). Miller et al.[6] suggested that the total damage to fisheries by California sea lions was not proportional to the number of sea lions in the area. It is likely that takes on a given day in Monterey Bay were repeat occurrences by the same animals. We agree with DeMaster et al. (1982) that a reduction in the number of animals or culling of the population would probably not reduce sea lion depredation levels unless the few animals responsible were identified and removed. Instead, there is a need for nonlethal deterrents to keep sea lions from taking hooked fish in open-ocean fisheries. A change in types of fishing gear, a limit in the amount of gear in the water, use of various harassment techniques, as well as area closures and a tolerance for sea lion predation most likely encompass other possible management options.

An increasing sea lion population and increased interactions with salmon fisheries resulting in salmon and gear losses will certainly affect individual fishermen negatively and possibly California's economy (Beeson and Hanan[1]). Comparisons of economic losses between years and among studies must consider average fish weight, exvessel price per year, and definitions of fishing regions. For example, if greater numbers of fish were lost in a given year but exvessel prices were low, the overall economic impact would be less than during a year when fewer fish were taken but the exvessel prices were high.

In past studies, all ports in California were surveyed, and impacts were analyzed by port, but these studies encompassed different fishing areas under the same port names. For example, Miller et al.[6] estimated annual losses resulting from sea lion interactions in 1980 at $274,000 for California, and an estimated $21,536 for Monterey Bay. It is unclear, however, if these figures included fishing areas south of Monterey, such as Morro Bay, and fishing areas north, such as Half Moon Bay. Beeson and Hanan[1] estimated 86,900 fish or $1,734,000 was lost in 1995 because of sea lion interactions, and 48,000 fish were taken in Monterey, representing approximately $960,000. Beeson and Hanan[1] included the Port of Princeton in Half Moon Bay in figures reported for Monterey. Therefore, it was not possible to make direct comparisons among studies, but it appears that economic losses per individual fisherman have increased since the 1980s and will probably continue to increase if the sea lion population and interactions with salmon fisheries increase. Assessment of economic impacts of salmon fisheries in Monterey Bay in the present study was limited to gear and fish loss; however impacts are most likely widespread. For example, during the salmon season when interactions with sea lions are great, CPFV operators report that customers will cancel or postpone trips, which decreases the amount of money infused into the local economy from trip expenditures, including hotel stays, restaurants meals, and gas. Estimating the economic impact of sea lion interactions on the local economy of Monterey Bay was beyond the scope of our study.

Discussions about the competition between sea lions and fisheries tend to arouse controversy because of the complex mix of biological, economic, social, political, and moral factors involved (Harwood and Croxall, 1988). Fishermen claim regularly that their activities are regulated, whereas predation by marine mammals is unrestricted (Harwood, 1992). Although losses in Monterey Bay in 1998 were most likely anomalously large because of ENSO conditions, this anomaly offered little reassurance to those fishermen whose livelihoods were threatened. Growing sea lion populations have undoubtedly intensified competition with fisheries, but greater fishing effort, more sophisticated fish equipment and fisheries methods, and less than rigorous fisheries management is equally responsible. Segments of the American public find marine mammals appealing and demand that populations be protected; whereas other segments demand protection from economic ruin resulting from marine mammal-fishery interactions. Clearly, demands from both segments of the public must be addressed (Everitt and Beach, 1982). Continued research to assess and refine our understanding of food habits of marine mammals is essential, and incorporating this information into fisheries management is equally important. When conflicts between fisheries and marine mammals are identified, population management strategies and nonlethal deterrent solutions need to be developed. Any management solutions need to consider not only the specific interactions but also the ecosystem as a whole and the viewpoints of all segments of the public.

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Estimates of growth and comparisons of growth rates determined from length- and age-based models for populations of purple wrasse (*Notolabrus fucicola*)

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Abstract—Growth of a temperate reef-associated fish, the purple wrasse (*Notolabrus fucicola*), was examined from two sites on the east coast of Tasmania by using age- and length-based models. Models based on the von Bertalanffy growth function, in the standard and a reparameterized form, were constructed by using otolith-derived age estimates. Growth trajectories from tag-recaptures were used to construct length-based growth models derived from the GROTAG model, in turn a reparameterization of the Fabens model. Likelihood ratio tests (LRTs) determined the optimal parameterization of the GROTAG model, including estimators of individual growth variability, seasonal growth, measurement error, and outliers for each data set. Growth models and parameter estimates were compared by bootstrap confidence intervals, LRTs, and randomization tests and plots of bootstrap parameter estimates. The relative merit of these methods for comparing models and parameters was evaluated; LRTs combined with bootstrapping and randomization tests provided the most insight into the relationships between parameter estimates. Significant differences in growth of purple wrasse were found between sites in both length- and age-based models. A significant difference in the peak growth season was found between sites, and a large difference in growth rate between sexes was found at one site with the use of length-based models.

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Methods for estimating growth in wild fish stocks derive largely from two sources: 1) age-based models, such as the von Bertalanffy growth function (VBGF), from data for length-at-age, where fish ages are known or estimated from scales, otoliths, and other hard parts; and 2) length-based models, from recapture data from tagged fish to describe a growth trajectory over time at liberty (e.g., Fabens, 1965), or analysis of modal progressions in length-frequency data (e.g., MULTIFAN, Fournier, et al., 1990). Many of these models seek to characterize growth of the population in terms of the three standard von Bertalanffy parameters, *viz.* l_∞, the theoretical asymptotic mean length; k, the growth rate coefficient; and t_0, the theoretical age at length zero.

Despite its wide use in descriptions of fish growth, the standard VBGF is often criticized because the function's parameters may represent unreasonable extrapolations beyond available data and hence lack biological relevance (e.g., Knight, 1968; Roff, 1980; Francis, 1988a; 1988b), estimates of l_∞ produced by standard length- and age-based versions of the model lack mathematical equivalence (e.g., Francis, 1988b; 1992), the statistical properties of the parameters make comparisons between samples difficult (Ratkowsky, 1986; Cerrato, 1990; 1991), and individual variability introduces biases in parameter estimates (Wang, et al., 1995; Wang and Thomas, 1995; Wang, 1998; Wang and Ellis, 1998).

These criticisms have led to various reparameterizations of the VBGF (see Ratkowsky, 1986; Cerrato, 1991 for examples). Analyses of reparameterizations for age-based VBGFs indicate that the inclusion of parameters that are expected lengths-at-age, for age classes drawn from the data set, dramatically improve the statistical properties of the model (Cerrato, 1991) and also result in parameters that have direct biological interpretation. Reparameterizations that fit this criterion include the reparameterization of the Francis (1988b) model for length-at-age data, and GROTAG, a reparameterization of the Fabens model from tagging data with expected growth rates for length as parameters (Francis, 1988a). GROTAG in particular has the advantage of being readily parameterized to include seasonal growth terms, and, through the application of a likelihood function, can include estimators of measurement error, individual growth variability, and the proportion of outliers in a data set. It has been used to produce growth estimates for cartilaginous fishes (Francis and Francis, 1992; Francis, 1997; Francis and Mulligan, 1998; Simpendorfer, 2000; Simpendorfer, et al., 2000), bony fishes (Francis, 1988b; 1988c; Francis, et al., 1999), and bivalve mollusks (Cranfield, et al., 1996). Fitting of any growth model with maximum likelihood methods also permits straightforward application of LRTs in order to compare parameter estimates, and to deter-

mine optimal parameterization of models (Kimura, 1980; Francis, 1988a). Computationally intensive methods such as bootstrapping and randomization tests provide a nonparametric method for approximating probability distributions of growth parameter estimates (Haddon, 2001), for generating confidence intervals to test for differences between parameter estimates, and for visualizing relationships between parameters (Mooij, et al., 1999). Drawing together these methods, it is possible to fit growth models, to produce parameter estimates that are biologically interpretable, and to use tests that are robust for comparing populations.

The purple wrasse (*Notolabrus fucicola*) is a gonochoristic, site-attached, reef-associated fish, common on moderate to fully exposed coasts in southeastern Australia and New Zealand (Russell, 1988; Edgar, 1997). Both *Notolabrus fucicola* and its Australian congener, the blue-throated wrasse (*N. tetricus*), are large benthic carnivores that play a significant role in the trophic dynamics of temperate reef systems (Denny and Schiel, 2001; Shepherd and Clarkson, 2001).

The development of a live fishery for *N. fucicola* and *N. tetricus* in southeastern Australia has made temperate wrasses increasingly important economically (Lyle[1]; Smith, et al.[2]).

Most previous attempts to describe the growth of *N. fucicola* (Barrett, 1995a; 1999; Smith, et al.[2]) have been compromised by small sample sizes, lack of age validation, and the use of unsuitable statistical models to compare length-at-age between populations. Ewing et al. (2003) recently validated an aging method and developed growth models for *N. fucicola*, combining samples from many sites from eastern and southeastern Tasmania. Our study describes site- and sex-specific age- and length-based models for this species. We also compare methods for examining differences in growth model parameter estimates, such as confidence intervals and randomization tests based on bootstrap estimates, plots of bootstrap estimates, and LRTs where comprehensive coverage of age and length data is unavailable—a situation commonly faced in fisheries.

Materials and methods

Field methods

Notolabrus fucicola were trapped and tagged at two sites on the east coast of Tasmania. Trapping was conducted at 1–2 month intervals, between July 1999 and April 2001 at Lord's Bluff (42.53°S, 147.98°E), and between July 2000 and March 2001 at Point Bailey (42.36°S, 148.02°E). Standard T-bar tags were inserted between the pterygiophores in the rear portion of the dorsal fin. Total length of each fish was recorded prior to release. Because *N. fucicola* display no external sexual characters, sex of fish could only determined by the presence of extruded gametes if fish were running ripe when captured, or by dissection at the conclusion of the study.

At the conclusion of the tag-recapture study, each site was fished intensively. Recaptured tagged fish were euthanized by immersion in an ice-slurry. Fish captured at Lord's Bluff were measured immediately after sacrifice; gonads were dissected to determine sex, and sagittal otoliths were collected. Untagged fish were returned immediately; therefore otoliths that were analyzed came from tagged fish only. All fish captured at Point Bailey were processed in a similar fashion but were stored frozen prior to examination.

Otolith preparation and interpretation

Sagittal otoliths were mounted in a polyester resin block, and transverse sections (250–300 μm thick) were cut through the primordium with a lapidary saw. Sections were mounted on a slide and examined under a binocular microscope at ×25 magnification. The primary author counted annuli and individuals were allocated to a year class, and fractional ages were assigned based on an arbitrary birthdate of 1 October, following the method of Ewing et al. (2003).

To determine if any significant differences existed within or between reader estimates, a random subsample of 55 otoliths, from both sites, was re-aged by the primary reader (DW) and another experienced otolith reader (GE). The frequency distribution of ages in each population was then compared with a Kolmogorov-Smirnov test. Consistency of age estimates was also compared by using age bias plots (Campana, et al., 1995) and the index of average percent error (IAPE *sensu* Beamish and Fournier, 1981).

Preliminary inspection of the length data for thawed individuals from Point Bailey revealed many negative growth increments when compared to length data collected from recaptures prior to the conclusion of field sampling. Repeated measurements of *N. fucicola*, conducted independently of our study, have shown length changes in the order of 8–9% in frozen and thawed individuals compared to measurements from individuals alive or freshly euthanized (G. P. Ewing, unpubl. data[3]). Consequently, measurements taken from frozen fish were deemed to be incompatible with measurements taken from fresh fish and were removed from the tagging and otolith data sets. Where data from

[1] Lyle, J. M. 2003. Tasmanian scalefish fishery—2002. Fishery Assessment Report, 70 p. Tasmanian Aquaculture and Fisheries Institute, Marine Research Laboratories, Univ. Tasmania, Nubeena Crescent, Taroona, Tasmania 7053, Australia.

[2] Smith, D. C., I. Montgomery, K. P. Sivakumaran, K. Krusic-Golub, K. Smith, and R. Hodge. 2003. The fisheries biology of bluethroat wrasse (*Notolabrus tetricus*) in Victorian waters. Draft Final Report, Fisheries Research and Development Corporation No. 97/128, 88 p. Marine and Freshwater Resources Institute, 2a Bellarine Highway, Queenscliff, Victoria 3225, Australia.

[3] Ewing, G. P. 2002. Unpubl. data. University of Tasmania, Tasmanian Aquaculture and Fisheries Institute, Marine Research Laboratories. Nubeena Crescent, Taroona, Tasmania 7053, Australia.

multiple recaptures allowed, the initial length and penultimate length measurement and their corresponding dates were used in length-based analyses at this site. Individual length-at-age estimates were also adjusted according to the date of any previous reliable length record.

Age-based growth modeling

Data consisted of ages estimated from otoliths (T) and lengths at final recapture (or last reliable length measurement at Point Bailey) (L). Kolmogorov-Smirnov tests were conducted between sites and between sexes within sites to determine if there were differences between the proportional frequency distributions of fish lengths in length-at-age data sets. Growth was modeled by using the standard von Bertalanffy growth function (VBGF):

$$L = l_{\infty}[1 - e^{-k(T-t_0)}]. \quad (1)$$

The VBGF for the two sites and sexes within sites were modeled separately (Table 1). Fish for which sex could not be determined were not included in the sex-specific models.

A reparameterized version of the VBGF was also estimated from Equation 4 in Francis (1988b):

$$L = l_{\tau} + \frac{[l_{\upsilon} - l_{\tau}][1 - r^{2(T-\tau)/(\upsilon-\tau)}]}{1 - r^2}, \quad (2)$$

$$\text{where } r = \frac{l_{\upsilon} - l_{\omega}}{l_{\omega} - l_{\tau}} \quad (3)$$

and where l_{τ}, l_{υ} and l_{ω}, are the mean lengths at ages τ, υ, and $\omega=(\tau+\upsilon)/2$—ages chosen from within the observed range within the data set. The values chosen for all the otolith-based models were $\tau=4$, $\omega=7$ and $\upsilon=10$ years, encompassing the range of ages represented in the data sets for both sites. Estimates of these parameters have a direct biological meaning and have more statistically favorable properties than the standard VBGF parameters l_{∞}, k, and t_0 (Francis, 1988b; Cerrato, 1991).

Models were fitted by minimizing a likelihood function and assuming normally distributed residuals (Eq. 4):

$$-\lambda = -\sum_i \ln\left(\frac{1}{\sqrt{2\pi}\sigma}\exp^{\frac{-(L_i-\mu_i)^2}{2\sigma^2}}\right). \quad (4)$$

The measured length of the i^{th} fish, L_i, has its corresponding expected mean length at age μ_i, as determined from Equation 1 or 2 above, where μ_i is normally distributed and has a standard deviation σ. The quality of the fits was gauged visually in the first instance by the lack of trends in plots of residuals against length-at-age.

To further investigate each model, each data set was bootstrapped 5000 times. The bootstrapping procedure involved randomly resampling, with replacement, from the original data set, and then fitting the VBGF to this new data set, thereby generating new estimates of all model parameters (Haddon, 2001).

Based on the percentile distribution of bootstrap parameter estimates, 95% confidence intervals (CIs) around the original sample estimates were calculated for each VBGF parameter. To account for any skew in the distribution of bootstrap parameter estimates, a first-order correction for bias of CIs was performed, where bootstrap percentiles used to estimate the CIs were adjusted on the basis of the proportion of bootstrap estimates less than the original estimate (Haddon, 2001).

To determine whether growth showed any site or sex-within-site (referred to as "sex-") differences, we compared the overlap of first-order corrected CIs and plots of bootstrap estimates. Simple comparison of CI overlap as a test for parameter difference has been shown to be overly conservative (Schenker and Gentleman, 2001). Hence the null hypothesis of no difference was accepted in the first instance only in cases were the amount of overlap was obviously large. In cases were the extent of overlap was small, and the chance of incorrectly accepting the null hypothesis existed, a randomization test was performed. This test involved constructing the distribution of the difference between the estimates of the parameter of interest. Parameter estimates were randomly selected with replacement from each set of bootstrap estimates for the two populations, and the differences were determined for these 5000 random pairs. Then a 95% first-order corrected CI was constructed as above, and the null hypothesis was rejected only if the CI did not include zero. Likelihood ratio tests were also conducted on the VBGFs and individual parameters (Kimura, 1980).

Length-based growth modeling

Growth trajectories consisted of the initial length (L_1), time at first capture (T_1), time at final recapture (or penultimate recapture at Point Bailey) (T_2), change in length from the first to the final recapture (ΔL), and duration in years between capture and last recapture (ΔT). T_1 and T_2 were measured in years from an arbitrarily chosen point, 1 January 1999—the first day in the earliest year in which tagging was conducted. For individuals recaptured more than once, only information relating to the initial and final captures was used in the analyses. This approach maximized the time between recaptures for any fish, increasing the chance of detecting growth, and gave equal weight to each fish sampled.

Because the two sites were sampled over different time periods, only samples from Lord's Bluff that were taken at the same time as samples at Point Bailey were considered for the purposes of between-site growth comparisons (Table 1). The resulting data set, designated LB_{res}, reduced potentially confounding effects of longer sampling durations at Lord's Bluff.

Table 1

Main model types (GROTAG and von Bertalanffy growth function [VBGF]), data sets, and sample sizes used to produce estimates of growth for *Notolabrus fucicola*. LB= Lord's Bluff, full data set; LB_{res}= Lord's Bluff, only fish captured over dates equivalent to the Point Bailey sample; PB=Point Bailey, full data set; ♂♂=males only; ♀♀=females only; *n*=sample size. The asterisk refers to one individual in this data set that was identified as an outlier during model parameterization and was excluded from bootstrapping.

Model type	Data set	Total *n*
GROTAG	LB_{res}	174
	PB	263
	LB♂♂	103
	LB♀♀	69*
	PB♂♂	96
	PB♀♀	89
VBGF	LB	101
	PB	178
	LB♂♂	47
	LB♀♀	54
	PB♂♂	68
	PB♀♀	104

A Kolmogorov-Smirnov test was conducted to determine whether differences existed in the proportional frequency distributions of lengths of fish at first capture (L_1) between sites and between sexes within sites.

Growth was modeled by using GROTAG (Eqs. 2 and 4 in Francis [1988a]), a reparameterization and extension of the Fabens growth model for tag-recapture data that incorporates seasonal growth:

$$\Delta L = \left[\frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} - L_1\right]\left[1-\left(1+\frac{g_\alpha - g_\beta}{\alpha-\beta}\right)^{\Delta T+(\phi_2-\phi_1)}\right], \quad (5)$$

$$\text{where } \phi_i = u\frac{\sin\left[2\pi(T_i - w)\right]}{2\pi} \text{ for } i = 1,2. \quad (6)$$

The parameters g_α and g_β are the estimated mean annual growth (cm/yr) of fish of initial lengths α cm and β cm, respectively, where $\alpha<\beta$. The reference lengths α and β were chosen such that the majority of values of L_1 in each data set fell between them (Francis, 1988a). For site-specific estimates of growth, α and β were set at 20 and 30 cm, respectively, whereas β was set at 28 cm for sex-specific models. Seasonal growth is parameterized as w (the portion of the year in relation to 1 January when growth is at its maximum) and u (u=0 indicating no seasonal growth through to u=1 indicating the maximum seasonal growth effect, i.e., where growth effectively ceases at some point each year).

Table 2

Parameters estimated in the five GROTAG models fitted to each tag-recapture data set to evaluate optimal model parameterization.

GROTAG model	Parameters estimated
1	g_α, g_β, v, p
2	$g_\alpha, g_\beta, v, p, u, w$
3	$g_\alpha, g_\beta, v, p, s, m$
4	$g_\alpha, g_\beta, v, u, w, s, m$
5	$g_\alpha, g_\beta, v, p, u, w, s, m$

The model was fitted by minimizing negative log-likelihood ($-\lambda$) function (Eq. 9 in Francis [1988a]). For each data set, made up of i = 1 to n growth increments:

$$\lambda = \sum_i \ln\left[(1-p)\lambda_i + p/R\right], \quad (7)$$

$$\text{where } \lambda_i = \exp\frac{-\frac{1}{2}(\Delta L_i - \mu_i - m)^2/(\sigma_i^2 + s^2)}{\left[2\pi(\sigma_i^2 + s^2)\right]^{\frac{1}{2}}}. \quad (8)$$

The measured growth increment of the i^{th} fish, ΔL_i, has its corresponding expected mean growth increment, μ_i, as determined from Equation 5 above, where μ_i is normally distributed with standard deviation σ_i. In this study, σ_i was assumed to be a function of the expected growth increment μ_i (Eq. 5, Francis, 1988a):

$$\sigma_i = v\mu_i. \quad (9)$$

where v is estimated as a scaling factor of individual growth variability, assuming a monotonic increase in variability around the mean growth increment as the size of the increment increases.

In its fully parameterized form, the likelihood function estimates the population measurement error in ΔL as being normally distributed, and having a mean of m and standard deviation of s. To estimate the proportion of outliers, Francis (1988a) also included p, the probability that the growth increment for any individual could exist erroneously in the data set as any value, within the observed range of growth increments R. This enables the proportion of outliers to be identified. Francis (1988a) suggested that an estimate of $p>0.05$ indicates a high level of outliers and therefore some caution would be required in interpreting the overall model fit.

The optimal model parameterization was determined by fitting five different models, comprising different

combinations of parameters (Table 2), with unfitted parameters held at zero. A LRT was used to determine the improvement in model fit with the different parameterizations (Francis, 1988a). For models with an equal number of parameters, the model producing the lowest negative log likelihood ($-\lambda$) was considered the best fit.

As with the otolith models, LRTs were conducted on the GROTAG models to compare between sites and sexes, and models were also bootstrapped 5000 times. First-order corrected 95% CIs were calculated for parameter estimates (Haddon, 2001), and pairwise comparisons of growth parameters, by using CIs and randomization tests, as described above for otolith-based models.

Results

Otolith interpretation

Kolmogorov-Smirnov tests showed no significant difference in age-frequency distributions generated by repeat readings of 55 otoliths by the primary reader ($D_{0.05}$=0.259, D_{max}=0.072, not significant) or between readers ($D_{0.05}$ =0.259, D_{max}=0.109, not significant). The IAPE score for all three readings was calculated as 6.9%, and no systematic under- or over-estimation of ages was apparent in age bias plots within or between readers. Therefore age estimates derived from the first readings by the primary author were used for modeling.

Age-based growth modeling

Site comparisons No significant differences in length frequencies were detected in a Kolmogorov-Smirnov test between sites ($D_{0.05}$=0.169, D_{max}=0.097, not significant).

Length-at-age estimates showed high variability among individuals, as evidenced by the spread of data points around the fitted models (Fig. 1), and estimates of σ ranged from 1.16 to 2.17 cm across all models (Table 3). However, mean lengths-at-age were adequately described by the VBGF across the ages represented by the samples from the two sites. The plots of the site-specific VBGFs indicated that mean length-at-age at Lord's Bluff was higher than at Point Bailey.

Because of the absence of young (0+ and 1+) fish in the samples from both sites, and fish >14+ at Lord's Bluff, the standard VBGF parameters were difficult to interpret biologically. Confidence intervals for the three standard VBGF parameters largely overlapped in comparisons between sites (Table 3). Plots of the bootstrap parameter estimates showed strong nonlinear correlations, particularly between l_∞ and k, revealing minimal overlap between sites, most easily visualized with logarithmic axes (Fig. 2A). Nonlinear correlation between parameter estimates and minimal overlap between sites were also true to a lesser extent in estimates of l_∞ versus t_0 (Fig. 2B). LRTs showed that differences between sites were highly significant overall

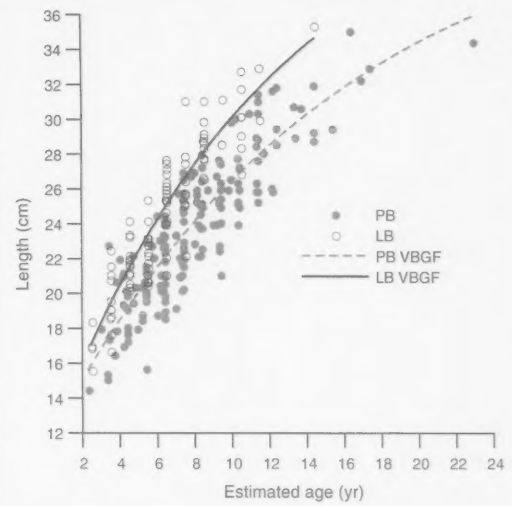

Figure 1

Length-at-age estimates for *Notolabrus fucicola*, derived from otoliths (symbols), and corresponding von Bertalanffy growth functions (VBGFs) fitted by least squares (lines). PB = Point Bailey, LB = Lord's Bluff.

but could not be attributed to significant differences in individual parameters (Table 4).

Confidence intervals for the Francis (1988b) reparameterized version of the VBGF clearly indicated significant differences in growth rates between sites in all three parameters, and no overlap between sites in the CIs of the estimates of mean length at 4, 7, or 10 years old (Table 3). These differences were also evident in plots of bootstrap parameter estimates, the two sites being clearly separated in the parameter space, and showed none of the high nonlinear correlations evident in the standard VGBF estimates (Fig. 3B). Randomization tests produced CIs of the difference between sites of 1.16–2.67, 2.48–3.50, and 2.82–4.44 cm for l_4, l_7, and l_{10}, respectively. Highly significant differences in all individual parameters growth parameters in the reparameterized model were also shown in LRTs between sites, but no significant difference in σ was detected (Table 4).

Sex comparisons Confidence intervals for the standard and reparameterized von Bertalanffy parameters significantly overlapped in all comparisons between sexes (Table 3). Likelihood ratio tests showed no significant differences between models of sexes within sites—a conclusion supported by considerable overlap in plots of bootstrap estimates (not shown).

Length-based growth modeling

Model parameterization Site-specific data sets were optimally parameterized under the most complex model,

Table 3

Von Bertalanffy growth function parameter estimates for *Notolabrus fucicola*. Numbers in bold text are parameter estimates from the original dataset. Numbers in parentheses are the proportion of parameter estimates from bootstrapped data sets that were less than the estimate from the original data set. Numbers in plain text are first-order corrected bootstrap 95% confidence intervals. LB = Lord's Bluff; PB = Point Bailey.

	Parameter estimate						
Dataset	l_∞ (cm)	k (/yr)	t_0 (yr)	l_4 (cm)	l_7 (cm)	l_{10} (cm)	σ (cm)
LB	**44.7**	**0.085**	**−3.23**	**20.4**	**25.9**	**30.1**	**1.61**
	(0.48)	(0.51)	(0.50)	(0.51)	(0.50)	(0.51)	(0.57)
	35.4 to 68.4	0.036 to 0.152	−5.82 to −1.59	20.0 to 20.9	25.4 to 26.3	29.4 to 30.8	1.39 to 1.87
PB	**43.3**	**0.065**	**−4.65**	**18.5**	**22.9**	**26.5**	**1.79**
	(0.66)	(0.51)	(0.50)	(0.52)	(0.53)	(0.58)	(0.32)
	37.9 to 86.7	0.021 to 0.096	−8.71 to −2.83	17.9 to 19.2	22.6 to 23.2	26.1 to 26.9	1.57 to 1.92
LB♂♂	**52.1**	**0.059**	**−4.46**	**20.3**	**25.5**	**29.7**	**1.38**
	(0.51)	(0.49)	(0.48)	(0.51)	(0.48)	(0.50)	(0.64)
	34.6 to 1210.1	0.001 to 0.157	−9.21 to −1.55	19.8 to 20.9	24.9 to 25.9	28.9 to 30.5	1.16 to 1.68
LB♀♀	**43.2**	**0.095**	**−2.80**	**20.5**	**26.1**	**30.4**	**1.74**
	(0.47)	(0.51)	(0.48)	(0.51)	(0.48)	(0.49)	(0.62)
	33.1 to 187.8	0.007 to 0.192	−7.42 to −0.98	19.9 to 21.3	25.5 to 26.7	29.2 to 31.7	1.45 to 2.17
PB♂♂	**43.3**	**0.060**	**−5.56**	**18.9**	**22.9**	**26.3**	**1.58**
	(0.47)	(0.52)	(0.51)	(0.54)	(0.53)	(0.55)	(0.60)
	33.3 to 163.3	0.007 to 0.138	−11.57 to −2.20	18.3 to 19.6	22.5 to 23.5	25.7 to 26.9	1.35 to 1.87
PB♀♀	**43.2**	**0.065**	**−4.60**	**18.5**	**22.9**	**26.5**	**1.91**
	(0.48)	(0.43)	(0.53)	(0.45)	(0.47)	(0.45)	(0.62)
	37.0 to 199.4	0.002 to 0.093	−10.61 to −2.35	17.6 to 19.3	22.5 to 23.3	25.9 to 27.0	1.73 to 2.16

incorporating seasonal growth and measurement error estimates (Table 5). Estimates of proportion of outliers in the data set (p) greater than zero were due to lack of fit and dropped to zero in model 5. Preliminary bootstrapping showed that fitting p regularly produced spurious model fits. Because the full data sets were estimated to have no outliers, it was considered reasonable to fit model 4 (equivalent to model 5, but with p held equal to zero) to all bootstrapped data sets for site-specific growth estimates and comparisons.

Table 4

Likelihood ratio tests of site differences in the von Bertalanffy growth functions fitted to *Notolabrus fucicola* length-at-age data and individual VBGF parameters, both standard and reparameterized. $-\lambda$ = negative log-likelihood. The base case represents the summed likelihood for both curves fitted separately.

Hypothesis	$-\lambda$	χ^2	df	P
Base case	553.0	—	—	—
Coincident curves	617.8	129.75	3	<0.001
$= l_\infty$	553.0	0.03	1	0.870
$= k$	553.2	0.36	1	0.548
$= t_0$	553.4	0.78	1	0.376
$= l_4$	565.7	25.47	1	<0.001
$= l_7$	602.9	99.78	1	<0.001
$= l_{10}$	589.2	72.53	1	<0.001
$= \sigma$	554.2	2.49	1	0.114

Estimates of p also dropped to zero in model 5 when this model was fitted to the sex-specific data sets, except for females at Lord's Bluff. Holding $p=0$ in model 4 for females at Lord's Bluff resulted in a less good fit compared to that of model 5 and also produced slightly different parameter estimates than those of model 5, namely increasing growth (g_{20} and g_{28}), growth variability (v), and measurement error (m) (Table 6). Visual inspection of residuals showed an obvious outlier in the data set. When this was removed and model 5 was refitted, p fell to zero and the other parameters estimates were very close to the values estimated from fitting model 5 to the original data set, and there was a large improvement in likelihood. Therefore the model for females at Lord's Bluff was based on the data set with the outlier excluded, and model 4 with p held at zero was fitted to all bootstrap data sets for sex-specific growth estimates and comparisons.

Site comparisons With the exception of s at Lord's Bluff, the proportion of bootstrap parameter estimates

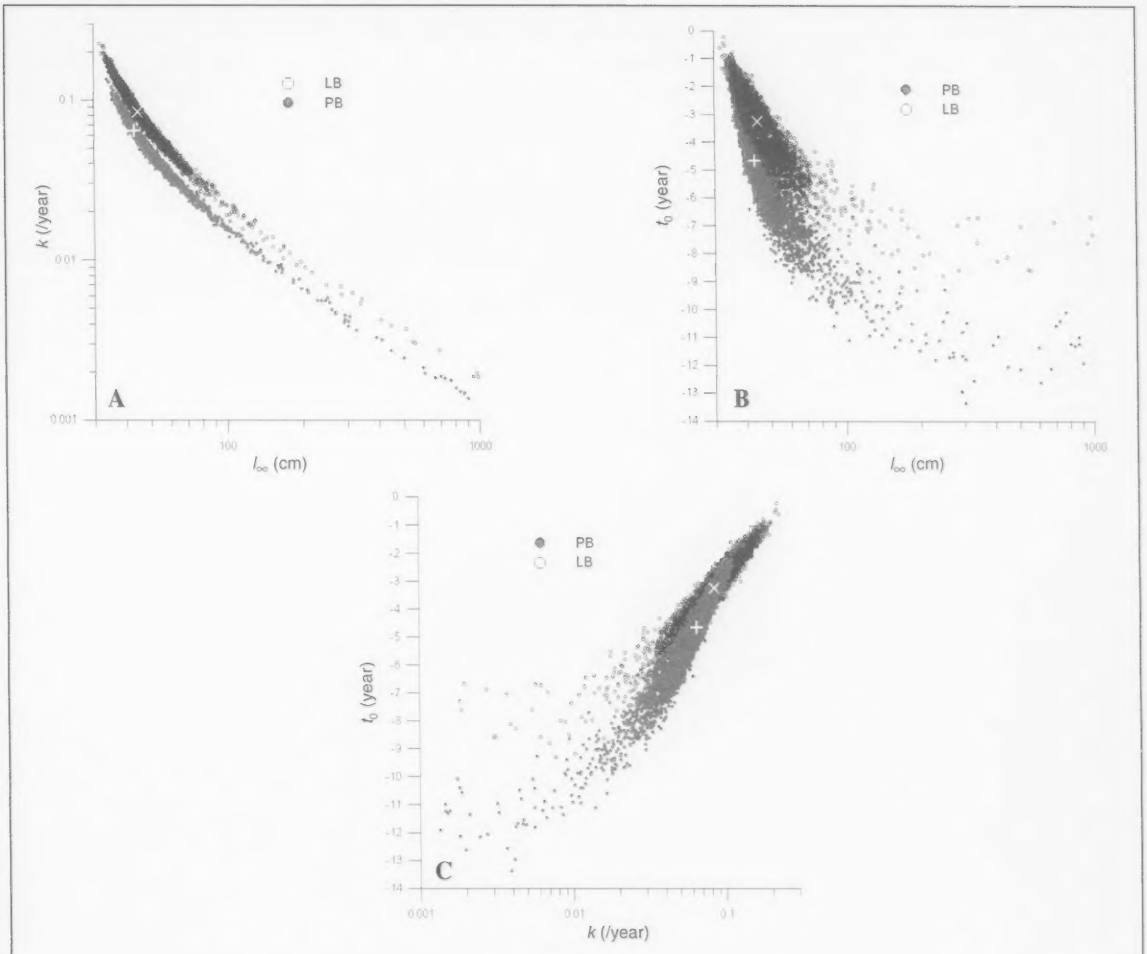

Figure 2

Bootstrap parameter estimates for *Notolabrus fucicola*, by site, for the standard von Bertalanffy growth function. Note l_∞ and k are plotted on logarithmic axes for clarity: (**A**) l_∞ vs. k (**B**) l_∞ vs. t_0 (**C**) k vs. t_0. Contrasting crosses show the location of parameter estimates based on the original data set (+, PB=Point Bailey, ×, LB= Lord's Bluff).

were more or less evenly distributed around the original parameter estimates, resulting in approximately symmetrical first-order corrected 95% CIs (Table 7). Based on the lack of overlap of CIs, only g_{20} differed significantly between sites. A randomization test of the difference in g_{20} produced CIs of 0.75–2.85 cm/yr faster growth at Lord's Bluff.

Plots of bootstrap parameter estimates clearly indicate differences in growth rates between sites, and little overlap in the parameter clouds along the g_{20} axis when g_{20} is plotted against g_{30} (Fig. 4A). Plots of bootstrapped estimates of the seasonal growth parameters u and w showed a high level of nonlinear correlation. A region of overlap between site estimates along the w axis is evident in Fig. 4B. However, the randomization test for this parameter produced a CI of the difference between the two sites of 0.02–0.33 yr, corresponding to significantly different maximum in seasonal growth occurring at Lord's Bluff 8–120 days after Point Bailey. Estimates of w at Point Bailey ranged from −0.14 to 0.05 years in relation to 1 January (Table 7), corresponding to peak growth between austral mid-spring and mid-summer (early November through mid-January), contrasting with the Lord's Bluff estimate of −0.08 to 0.20 years and indicating peak growth from austral late spring to early autumn (mid-December through mid-March).

Site differences in growth were also indicated in the results of LRTs. The overall models were significantly different; the growth parameter g_{20} and the timing of maximum seasonal growth were significantly different

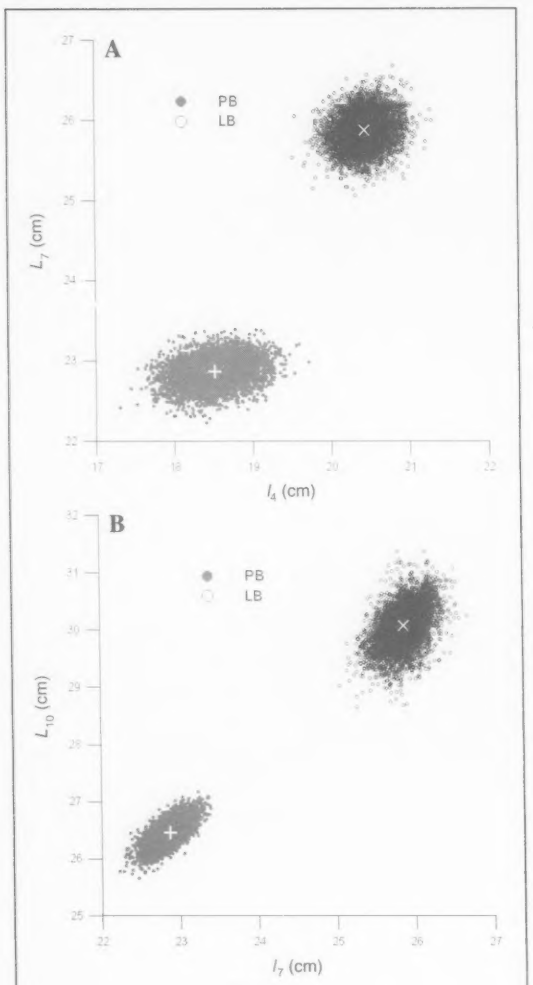

Figure 3

Bootstrap estimates of reparameterized von Bertalanffy growth function mean lengths at age for *Notolabrus fucicola*, by site. (**A**) l_4 versus l_7. (**B**) l_7 versus l_{10} mean length-at-ages at 7 and 10 years. Contrasting crosses show the location of parameter estimates based on the original data set (+, PB=Point Bailey, ×, LB=Lord's Bluff).

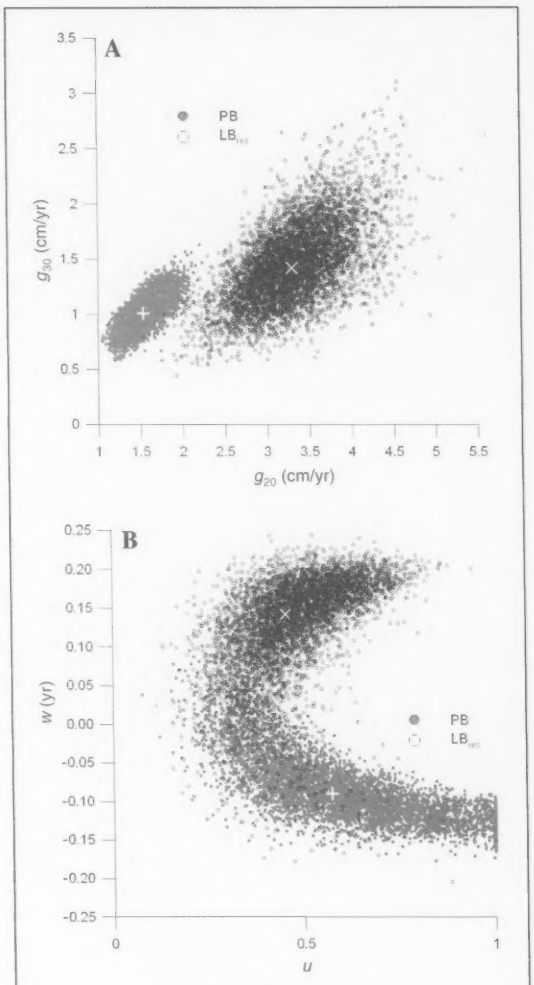

Figure 4

Bootstrap estimates of GROTAG parameters for *Notolabrus fucicola*, by site: (**A**) g_{20} versus g_{30}, mean annual growth at initial length 20 and 30 cm and (**B**) u versus w, magnitude and timing of seasonal growth. Contrasting crosses show the location of parameter estimates based on the original data set (+, PB = Point Bailey, ×, LB_{res}=Lord's Bluff).

at α=0.05 when tested individually (Table 8A), in agreement with the results of the randomization tests.

Sex comparisons Bootstrapped parameter estimates from sex-specific data sets were approximately symmetrical about the original estimates (Table 7). The largest divergence from 0.5 was evident in estimates of s for females at Lord's Bluff and males at Point Bailey. Bootstrap estimates of u for Lord's Bluff males occasionally extended into spurious negative values, lowering confidence estimates of the extent of seasonal growth in this data set (Table 7).

Based on simple overlap of CIs, no single parameter differed significantly between sexes at either site (Table 7). Plots of the bootstrap estimates of the growth parameters g_{20} and g_{28} showed minimal overlap between males and females, and separation was most evident along the g_{20} axis (Fig. 5A). Plots of bootstrapped estimates of the seasonal growth parameters u and w (Fig. 5B), and the measurement error parameters m and s

Table 5

Parameter estimates and negative log-likelihoods ($-\lambda$) of models used in likelihood ratio tests to determine the optimal parameterization of GROTAG models for *Notolabrus fucicola* tagging data, by site. Bold text in $-\lambda$ column indicates the optimally parameterized model for each data set. Model 4 is equivalent to model 5 with $p = 0$ in these instances. LB_{res} = residents of Lord's Bluff; PB = Point Bailey.

		Parameter estimate								
Data set	Model	g_{20} (cm/yr)	g_{30} (cm/yr)	v	u	w (yr)	s (cm)	m (cm)	p	$-\lambda$
LB_{res}	1	1.84	1.07	0.88	—	—	—	—	0.07	57.06
	2	3.00	1.67	0.88	0.59	0.22	—	—	0.07	50.46
	3	2.60	1.12	0.29	—	—	0.22	−0.12	0.00	20.59
	4 and 5	3.30	1.42	0.26	0.45	0.14	0.22	−0.10	0.00	**12.97**
PB	1	1.50	1.01	0.73	—	—	—	—	0.16	87.82
	2	1.55	1.15	0.82	0.31	0.13	—	—	0.07	79.02
	3	1.87	1.18	0.36	—	—	0.19	−0.08	0.00	36.16
	4 and 5	1.53	1.01	0.35	0.57	0.91	0.18	−0.07	0.00	**23.52**

Table 6

Parameter estimates and negative log-likelihoods ($-\lambda$) of models used in likelihood ratio tests to determine the optimal parameterization of GROTAG models for *Notolabrus fucicola* tagging data, by sex within site. Bold text in $-\lambda$ column indicates the optimally parameterized model for each data set. * indicates the parameter estimates and likelihoods when GROTAG is fitted to the Lord's Bluff (LB) ♀♀ data set with a single outlier removed. Model 4 is equivalent to model 5 with $p = 0$ in all other instances. PB = Point Bailey.

		Parameter estimate								
Data set	Model	g_{20} (cm/yr)	g_{30} (cm/yr)	v	u	w (yr)	s (cm)	m (cm)	p	$-\lambda$
LB♂♂	1	1.98	1.49	0.52	—	–	—	—	0.00	43.07
	2	1.88	1.54	0.50	0.23	0.04	—	—	0.00	39.24
	3	2.09	1.62	0.27	—	—	0.21	−0.05	0.00	32.21
	4 and 5	2.04	1.67	0.27	0.23	0.19	0.20	−0.04	0.00	**29.44**
LB♀♀	1	2.05	1.40	0.52	—	–	—	—	0.16	60.58
	2	1.99	1.20	0.48	0.41	0.98	—	—	0.15	58.19
	3	2.88	1.87	0.26	—	—	0.25	−0.29	0.00	41.15
	4	2.75	1.75	0.25	0.32	0.96	0.24	−0.31	—	38.40
	5	2.66	1.48	0.22	0.47	0.94	0.22	−0.26	0.03	36.23
	4 and 5*	2.66	1.48	0.22	0.48	0.94	0.23	−0.26	0.00	**30.36**
PB♂♂	1	1.31	1.02	0.60	—	—	—	—	0.24	21.31
	2	1.15	0.96	0.61	0.41	0.90	—	—	0.19	19.93
	3	1.54	1.21	0.33	—	—	0.19	−0.03	0.00	6.43
	4 and 5	1.15	0.93	0.32	0.81	0.88	0.18	−0.04	0.00	**2.49**
PB♀♀	1	1.49	1.15	0.68	—	—	—	—	0.16	30.55
	2	1.43	1.16	0.90	0.33	0.12	—	—	0.00	28.85
	3	1.96	1.32	0.38	—	—	0.20	−0.11	0.00	19.06
	4 and 5	1.46	1.01	0.39	0.77	0.87	0.18	−0.12	0.00	**15.78**

(Fig. 5C) showed distinct relationships within the two sexes. Randomization tests confirmed significant differences in g_{20}, m, and w. The CIs of these differences were estimated to be 0.2–1.09 cm/yr faster for females with an initial size of 20 cm, with an annual peak in female growth 3–152 days earlier than males, and with a measurement error that overestimated female length by 2–40 mm more than the measurement error for males.

Table 7

GROTAG parameter estimates derived from *Notolabrus fucicola* tag-recapture data. For all data sets, g_α is the mean annual growth of individuals with an initial length of 20 cm. g_β represents the estimated mean annual growth of individuals with an initial length of 30 cm for Lord's Bluff (LB_{res}) and Point Bailey (PB), or the estimate for 28-cm individuals for all other data sets. Numbers in bold text are the parameter estimates from the original data sets. Numbers in parentheses are the proportion of parameter estimates from bootstrap data sets less than the original estimate. Numbers in plain text are first-order corrected bootstrap 95% confidence intervals.

	Parameters estimate						
Data set	g_α (cm/yr)	g_β (cm/yr)	v	u	w (yr)	s (cm)	m (cm)
LB_{res}	**3.30**	**1.42**	**0.26**	**0.45**	**0.14**	**0.22**	**−0.10**
	(0.50)	(0.48)	(0.54)	(0.43)	(0.47)	(0.60)	(0.48)
	2.32 to 4.34	0.80 to 2.19	0.14 to 0.40	0.23 to 0.68	−0.08 to 0.20	0.18 to 0.26	−0.18 to −0.03
PB	**1.53**	**1.01**	**0.35**	**0.57**	**−0.09**	**0.18**	**−0.07**
	(0.51)	(0.51)	(0.50)	(0.46)	(0.54)	(0.55)	(0.56)
	1.21 to 1.94	0.76 to 1.31	0.27 to 0.44	0.25 to 1.00	−0.14 to 0.05	0.15 to 0.22	−0.12 to −0.01
LB♂♂	**2.04**	**1.68**	**0.27**	**0.23**	**0.19**	**0.20**	**−0.04**
	(0.48)	(0.51)	(0.58)	(0.45)	(0.48)	(0.57)	(0.49)
	1.77 to 2.31	1.32 to 2.01	0.20 to 0.40	−0.06 to 0.43	−0.02 to 0.29	0.12 to 0.28	−0.14 to 0.06
LB♀♀	**2.66**	**1.48**	**0.22**	**0.48**	**−0.06**	**0.23**	**−0.26**
	(0.49)	(0.50)	(0.50)	(0.39)	(0.52)	(0.62)	(0.49)
	2.27 to 2.98	1.18 to 1.83	0.13 to 0.30	0.16 to 0.69	−0.16 to 0.12	0.14 to 0.34	−0.41 to −0.10
PB♂♂	**1.15**	**0.93**	**0.32**	**0.81**	**−0.12**	**0.18**	**−0.04**
	(0.41)	(0.43)	(0.57)	(0.51)	(0.43)	(0.62)	(0.53)
	0.83 to1.69	0.61 to 1.41	0.17 to 0.47	0.18 to 1.00	−0.20 to 0.10	0.14 to 0.24	−0.14 to 0.06
PB♀♀	**1.46**	**1.01**	**0.39**	**0.77**	**−0.13**	**0.18**	**−0.12**
	(0.50)	(0.47)	(0.56)	(0.46)	(0.47)	(0.56)	(0.51)
	1.08 to 2.33	0.70 to 1.01	0.23 to 0.74	0.14 to 1.00	−0.20 to 0.14	0.09 to 0.27	−0.22 to 0.00

Table 8

Likelihood ratio tests of the GROTAG models for which bootstrap parameter estimates were generated (Tables 5 and 6): (A) Point Bailey (PB) against Lord's Bluff (LB_{res}) (B) LB♀♀ against LB♂♂. $-\lambda$= negative log-likelihoods. The base case is the negative log-likelihood of the data sets fitted with two wholly separate models. * = significant at α=0.05.

A Hypothesis	$-\lambda$	χ^2	df	P
Base case	36.49	—	—	—
Coincident curves	51.98	30.98	7	<0.001*
$=g_{20}$	42.19	11.38	1	<0.001*
$=g_{30}$	37.36	1.72	1	0.189
$=v$	37.35	1.72	1	0.190
$=u$	36.62	0.12	1	0.623
$=w$	38.91	4.84	1	0.028*
$=s$	37.64	2.28	1	0.130
$=m$	36.66	0.33	1	0.565

B Hypothesis	$-\lambda$	χ^2	df	P
Base case	59.80	—	—	—
Coincident curves	72.17	24.75	7	<0.001*
$=g_{20}$	63.43	7.27	1	0.007*
$=g_{28}$	60.21	0.83	1	0.362
$=v$	60.11	0.62	1	0.431
$=u$	60.64	1.69	1	0.194
$=w$	62.05	4.50	1	0.034
$=s$	59.94	0.30	1	0.583
$=m$	62.51	5.43	1	0.020*

These conclusions agreed with the LRTs, which indicated highly significant differences between g_{20} between sexes at Lord's Bluff, and significant differences between m and w at α=0.05 when tested individually (Table 8B). This contrasts with the results of age-based modelling of sex-specific growth at Lord's Bluff, where no difference between the sexes was detected in any test.

Sex comparisons at Point Bailey revealed no sex-specific growth differences, and neither CIs (Table 7)

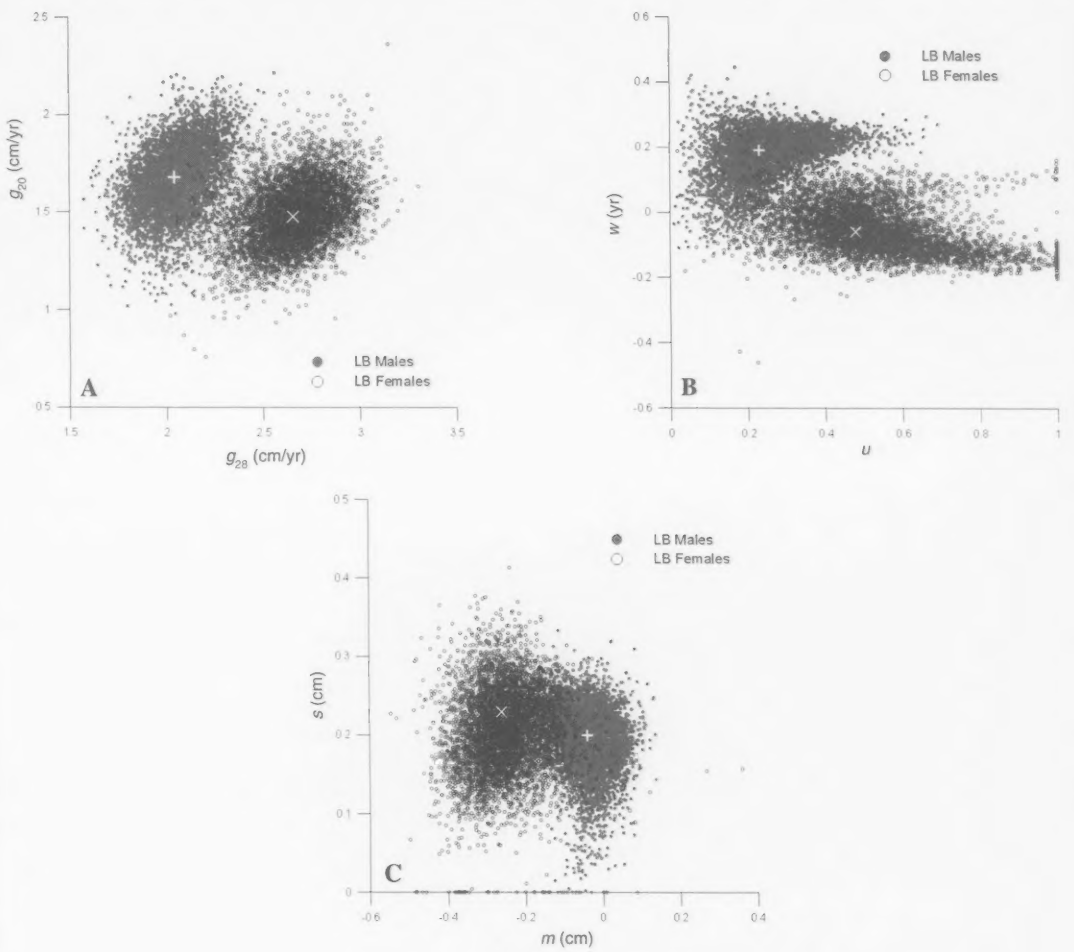

Figure 5

GROTAG bootstrap parameter estimates for *Notolabrus fucicola* from Lord's Bluff, by sex: (**A**) g_{20} versus g_{28}, mean annual growth at initial length 20 and 28 cm; (**B**) u versus w, magnitude and timing of seasonal growth and (**C**) m versus s, mean and standard deviation of measurement error. Contrasting crosses show the location of parameter estimates based on the original data set (+ = males, × = females).

nor LRTs indicated significant difference in any of the model parameters, and bootstrap plots showed large regions of overlap (not shown).

Discussion

Comparisons of models

In this study, two methods, based on mathematically different concepts, produced similar conclusions, namely that growth in *N. fucicola* was faster at Lord's Bluff than at Point Bailey. The results of length-based and age-based models also produced similar conclusions regarding the methods most suitable for robust comparisons of models and parameter estimates for different groups of fish. Confidence intervals were only reliable indicators of difference in cases where parameters showed low levels of correlation between estimates and where highly significant differences existed, such as in site comparisons of the reparameterized VBGF parameters, and hence were of limited utility.

Likelihood ratio tests provided a robust method of testing differences between models. However, we believe

that evidence from more than one source is required before conclusions can be drawn about differences between models designed to describe nonlinear processes such as growth. In the present study, bootstrapping techniques proved to be informative as a way of visualizing the behavior of the models used, and the distributions and correlations of parameter estimates that could not be determined readily from model likelihoods alone. They also provided a basis for estimating nonparametrically with randomization tests the differences, and CIs, of growth estimators between populations. Hence we recommend bootstrapping, plots of parameter estimates, and randomization tests to complement the "traditional" statistical tests such as the LRTs.

The standard VBGF has been criticized for the difficulty it causes in extracting biological meaning from parameters (Knight, 1968; Roff, 1980; Francis, 1988b; 1992). The problem is particularly acute where only a part of the size or age range (or both ranges) of animals is available—a situation regularly faced in analyses of fisheries data (Haddon, 2001). Data sets in our study were limited, particularly by the lack of fish in the lower age classes (*cf.* Ewing et al., 2003). Hence, any attempt to interpret or compare l_∞ or t_0 as descriptors of the growth of *N. fucicola* would be spurious. Furthermore, because k and l_∞ are highly correlated, comparisons of k cannot be independent of the effects of size or age selectivity on a data set. Because of the limitations of such parameters, and as l_∞ and k are often inputs into population dynamics models and empirical models estimating parameters such as natural mortality (e.g., Pauly, 1979), extreme caution should be exercised when extrapolating these values from limited data. However, this instance exemplifies the utility of the reparameterization, because even with limited data, the useful parameters of mean lengths at age can be estimated and compared.

Variability in growth

Models of growth can be used to estimate length-dependent processes in fish populations, such as reproductive output, increases in biomass due to individual growth, selectivity of fishing gear, and the impact and appropriateness of size limits as management tools. The results of the present study demonstrate that growth varies significantly across individuals, seasons, sexes, and sites in *N. fucicola*.

Although the significance of estimating the variability in growth around the population mean (v) was not explicitly tested during model parameterization, values of v around 0.2 to 0.7 were estimated for all data sets modeled. Values in this range have been estimated with GROTAG from other species of bony fishes (Francis, 1988a; b; 1988c; 1992; Francis, et al., 1999) and cartilaginous fishes (Francis and Francis, 1992; Francis, 1997; Francis and Mulligan, 1998; Simpendorfer, 2000; Simpendorfer, et al., 2000), indicating that considerable individual variability in annual growth of size classes is common. The extent of variability in individual growth is an important factor when quantifying growth because it may obscure other sources of growth variation, particularly in situations where data are limited. This effect may partially explain why age-based models failed to detect any significant effect of sex on growth rates in our study, whereas length-based modeling indicated that among smaller size classes, females grew faster than males at Lord's Bluff. On the basis of a large data set (>1000 individuals), Ewing et al. (2003) demonstrated that average length-at-age was significantly higher for females than males in *N. fucicola* although the magnitude of this difference was small. No growth differences between the sexes were evident at Point Bailey but given slower growth rates, the absolute magnitude of any expected growth differences related to sex would be relatively small and difficult to detect statistically.

Our study is the first to show that growth rates of *N. fucicola* vary significantly across small spatial scales; the two sites in our study were separated by less than 25 km. At Point Bailey, few individuals reach the minimum legal size limit of 30 cm until 10 years of age, whereas at Lord's Bluff they do so at least two years earlier (Fig. 1). An equivalent conclusion is evident from the GROTAG estimates, indicating that a 28-cm fish at Point Bailey will take nearly 2 years on average to exceed 30 cm, whereas fish of the same size are likely to reach legal size in just over a year at Lord's Bluff. Hence relative yields and rates of replacement of recruited size and age classes are likely to be lower at Point Bailey than at Lord's Bluff. However, because *N. fucicola* can be sexually mature at lengths of 12 cm (Patterson, 2000), some individuals are likely to have spawned for 6–8 years before recruitment to the fishery at Lord's Bluff (Fig. 1). This size at maturity suggests that the minimum legal size limit provides effective protection of the reproductive output of the prerecruit population of *N. fucicola* at both sites.

Using length-at-age estimated from whole otoliths, Barrett (1999) found no growth differences between several populations of *N. fucicola* in southeastern Tasmania and used these findings to support the hypothesis that populations are not resource limited. Our study did not specifically address any hypothesis about resource limitation but has clearly demonstrated that growth rates can vary between populations at the scale of individual reefs. *Notolabrus fucicola* are site-attached once they settle out of the plankton, rarely having an ambit of more than 500 m on contiguous reef, and rarely crossing soft bottom habitat if they are resident on smaller patch reef habitat (Barrett, 1995b). Intuitively, it follows that if productivity varies between reefs, then the potential for growth of individual site-attached reef fish may be limited. A variety of factors have been cited in other temperate reef species where spatial variability in length-at-age is evident, such as habitat type (Gillanders, 1997; Barrett, 1999), conspecific competition and variation in juvenile recruitment (Jones, 1980, 1984), and impacts of exploitation (Buxton, 1993). Further study is advocated to determine the factors that influence *N. fucicola* growth at this scale.

Parameterization of seasonal growth significantly improved the fit of the GROTAG models, indicating that seasonal variability in growth is significant for *N. fucicola*. The estimates of seasonal growth from our study constitute the first for this species. The LRTs indicated significant differences in the timing of maximum growth (w) between sites and between sexes at Lord's Bluff. This result was repeated in the randomization tests based on the outputs of bootstrapping. Peak growth in *N. fucicola* at both sites is estimated to occur over the austral spring–summer, during maximum water temperatures and increased productivity off the coast of Tasmania (e.g., Halpern, et al.[4]), and peak growth occurs significantly later in the season at Lord's Bluff than at Point Bailey. The mechanism affecting the timing of seasonal growth at this reef-by-reef scale is worthy of further investigation but is likely to include variability in seasonal cycles of oceanography, in availability of food (Denny and Schiel, 2001; Shepherd and Clarkson, 2001) and in temperature effects on metabolism, controlling the amount and timing of resources for allocation to growth throughout the year.

The estimate of the size of the difference in w between the sexes at Lord's Bluff had very broad CIs, and it is difficult to propose a hypothesis that could result in seasonal growth varying between the sexes by as much as five months, although resource allocation for reproduction could be involved. It may be that the particularly small size of the female data set at this site limited our ability to estimate seasonal growth accurately with GROTAG, and further study is required to more precisely determine how important seasonal growth differences between the sexes are in temperate reef fishes such as *N. fucicola*.

Sex-specific GROTAG analyses indicated a significant difference in measurement errors; females were under measured by a mean of 3 mm, compared to less than 1 mm for males at Lord's Bluff. Greater measurement errors for females have been detected in other studies with GROTAG (e.g., Simpendorfer, 2000), but a reason for greater difficulty in measuring females is difficult to determine. A possible explanation from our study is the high individual growth variability and small sample sizes. Both of these factors have been shown to affect accurate estimation of measurement error in GROTAG (Francis and Mulligan, 1998), and therefore the high estimate of m in our study may be an artifact of the data set.

A significant difference in growth between the sexes at Lord's Bluff indicates that under conditions of rapid growth, females may grow significantly faster than males. As discussed above, the current minimum legal size limit is effectively protecting the reproductive output of the prerecruit population of *N. fucicola*. However, any significant lowering of the legal minimum size is contraindicated where, in prerecruitment size classes, females grow more rapidly than males, because lowering the legal size may result in differences in sex-specific fishing mortality.

As demonstrated in the present study, the choice of growth model and the methods used to compare parameter estimates are critical to ensuring that growth is adequately described, differences in growth are detected, and if detected, are interpretable. In combination, the tests we employed are shown to be generally robust, even in situations where data sets are limited in sample size or by coverage across the full range of age and length classes. We recommend the use of a combination of approaches, including growth models with biologically interpretable parameters, statistical tests such as LRTs, plots of bootstrap parameters, and nonparametric randomization tests, to provide insight into the growth dynamics of fish species.

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Effects of harvesting methods on sustainability of a bay scallop fishery: dredging uproots seagrass and displaces recruits

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Fishing is widely recognized to have profound effects on estuarine and marine ecosystems (Hammer and Jansson, 1993; Dayton et al., 1995). Intense commercial and recreational harvest of valuable species can result in population collapses of target and nontarget species (Botsford et al., 1997; Pauly et al., 1998; Collie et al. 2000; Jackson et al., 2001). Fishing gear, such as trawls and dredges, that are dragged over the seafloor inflict damage to the benthic habitat (Dayton et al., 1995; Engel and Kvitek, 1995; Jennings and Kaiser, 1998; Watling and Norse, 1998). As the growing human population, over-capitalization, and increasing government subsidies of fishing place increasing pressures on marine resources (Myers, 1997), a clear understanding of the mechanisms by which fishing affects coastal systems is required to craft sustainable fisheries management.

Dredging, possibly the most destructive of common fishing methods (Collie et al., 2000), has been the subject of many recent ecological studies (Dayton et al., 1995; Jennings and Kaiser, 1998; Thrush et al., 1998). These studies indicate that dredge extraction and disturbance can have large direct effects on the abundance, biomass, and diversity of resident macrobenthic species (e.g., Caddy, 1973; Eleftheriou and Robertson, 1992). In addition, dredging can indirectly affect macrobenthic species through disturbance of benthic habitat (Ramsay et al., 1998; Lenihan and Peterson, 1998). Indirect impacts of dredging may be particularly serious where highly structured biogenic habitats, such as oyster reefs or seagrass beds, are affected (Peterson et al., 1987; Lenihan and Peterson, 1998; Collie et al., 2000; Lenihan and Peterson, 2004). These habitats may be considered essential habitat for many species of fish of commercial or recreational value (Thayer et al., 1975), providing refuges from predators (Orth et al., 1984; Castel et al., 1989) and abundant epibiotic food (Virnstein et al., 1984; Sánchez-Jerez et al., 1999).

Among fishery species dependent on biogenic habitat is the commercially and recreationally important bay scallop (*Argopecten irradians*). In the two reproductive seasons, spring and fall, bay scallop recruits settle onto hard substrates (Belding, 1910; Castagna, 1975) where they remain attached for the first few months of their lives. They then complete their 12–24 month life cycle on the estuary floor. In North Carolina, eelgrass is the only hard substrate of any abundance to which bay scallop recruits can attach themselves (Kirby-Smith, 1970).

Commercial harvest of bay scallops in North Carolina is achieved primarily by toothless epibenthic dredge (22.7 kg legal limit; NCFMC[1]). Dredges have the advantage that, unlike rakes, they can be used from boats in deep as well as shallow waters. Their disadvantage is that they decrease the biomass and shoot density of seagrass in scallop beds (Fonseca et al., 1984). Early in the North Carolina scallop season, which extends from December through May (NCMFC[1]), most of the juveniles from the previous fall spawning are still attached to seagrass blades (Spitsbergen[2]). If these juveniles are displaced by habitat destruction, reduced numbers of scallops may be available for harvest in the subsequent year (hypothesized by Thayer and Stuart, 1974). Although seagrasses can recover from small-scale disturbances to shoots by vegetative growth, large-scale disturbances to their subsurface root and rhizome system may permanently reduce the density of submerged aquatic vegetation (SAV) (Peterson et al., 1987) such that it may limit settlement of the following year's recruits or induce greater rates of predation on them (or bring about both). Although, in North Carolina, the bay scallop fishery management plan requires that the scallop season be opened after fall spawning is completed (Peterson, 1990); it fails to consider how methods of harvest may indirectly effect spawning stock biomass in years to come.

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Implementation of gear restrictions that allow only hand methods of harvesting scallops (i.e., hand, rake, dip nets) may minimize impacts of harvesting on scallop recruits by reducing damage to seagrass and the loss of juvenile bay scallops that comprise the year class that will be fished in the following year. Although such restrictions were introduced to Bogue Sound in 1992 in response to the 1987 red tide that decimated scallop populations in that water basin (Summerson and Peterson, 1990), this conservation-based measure was discontinued in 1998 because of social pressure from fishermen. In the present study, we ascertain the impacts of dredges and hand-harvesting methods on the biomass of seagrass, as compared to undisturbed controls, 1) by measuring the biomass of seagrass directly dislodged by each method, and 2) by ascertaining, through measurements of biomass one month later, whether this removal affects the standing stock of seagrass over a longer temporal scale. We also tested both direct and indirect effects of seagrass removal on bay scallop recruits by measuring their density before and one month after harvesting and by ascertaining whether any documented difference can be explained by the numbers directly removed by uprooting of seagrass during harvesting. Such an assessment of ecological impacts of dredging on bay scallop recruits is urgently required given that North Carolina landings of bay scallops have fallen to an historic low since the relaxation of gear restrictions (Burgess and Bianchi[3]).

Materials and methods

Nine adjacent experimental plots, 25 m × 8 m, were established as a research sanctuary, closed to commercial fishing activity, in western Bogue Sound, North Carolina (34°41.6′N, 76°59.1′W), prior to the opening of the scallop season in winter 2001–2002. Although this section of Bogue Sound has been closed to scallop dredging since at least 1998, its high-tide water depth of 1.5 m is well within the depth range for harvesting with this method. Plots contained continuous seagrass beds dominated by *Zostera marina* on a muddy-sand bottom. Three of the plots were randomly assigned to each of the experimental treatments: hand-harvested, dredge-harvested, and control (undisturbed). In order to ensure that our treatments were representative of harvesting methods and intensities used by the industry, they were performed with participation of an experienced commercial scallop fisherman (Ted Willis of Salter Path). Dredging was achieved with a standard 72-cm wide steel scallop dredge, at an intensity of five parallel tows, each running along the length of the plot within a 10-minute period. This method, which mimicked commercial fishing practices, minimized overlap between the dredge paths. Hand scalloping involved a single fisherman collecting scallops from the bottom by hand, also during 10-minute periods. Care was taken to ensure that the treatments were applied evenly over the entire plot to avoid creating large within-plot variance that might preclude detection of differences among plots.

Seagrass and scallops collected during harvesting were retained for measurements. The number of adult scallops (>40 mm shell height; Peterson et al., 1989) obtained with each of the methods of harvest was enumerated. The size (to the nearest 0.1 mm) and number of juvenile scallops collected as bycatch and the dry weight of seagrass removed during harvesting were quantified separately. Because not all seagrass and juvenile scallops displaced by harvesting are retained in the dredge or by a fisherman collecting scallops by hand methods, an 8-m long net with 5-mm mesh that extended from the bottom to the surface was set downstream from each plot and perpendicular to the flow of the current during harvest. The nets were strung between stakes marking the corners of the experimental plot. Dislodged juvenile scallops and seagrass collected by the nets were added to the amounts extracted from the dredge to compute displacement totals. Nets were also set downstream of controls to determine natural rates of transport of seagrass and juvenile scallops that could not be attributed to harvesting operations.

Each plot was sampled on 14 January 2002, immediately prior to harvesting on that same day to determine: 1) the density of bay scallop recruits (size ≤40 mm; Peterson et al., 1989); 2) the size distribution of the recruits; and 3) biomass per unit of area of seagrass. These variables were resampled on 25 February 2002, over one month later, to ascertain any lasting impact of harvest. Sampling of scallops was conducted with a 0.5-m^2 cylindrical quadrat, haphazardly positioned at nine locations within each plot. A 1.2-cm tall cylinder of 6-mm nylon mesh, attached to the quadrat and suspended by a buoyant plastic hoop that floated on the surface of the water, isolated the volume of water above each quadrat so that it could be sampled by suction with a Venturi suction device (according to Peterson et al., 1989). The suction device forced 600 mL of water per minute through a 3-mm collecting bag. Suction sampling was necessary because scallops, which typically recline on the bottom, can enter the water to swim when threatened by predators or otherwise disturbed (Peterson et al., 1982). The disturbance caused by suction sampling of only nine small areas was minimal compared to the scale of harvesting disturbance. Upon returning to the laboratory, seagrass was removed from samples for measurement of dry weight biomass and live scallops were counted, measured to the nearest 0.1 mm and categorized as adults (>40 mm) or recruits (≤40 mm) in the subsequent year class.

Seagrass was sampled in five replicate 0.25-m^2 areas within each plot by suction dredging inside a 0.56-m diameter circular quadrat to a sediment depth of 12 cm. Previous sampling has shown this method to be success-

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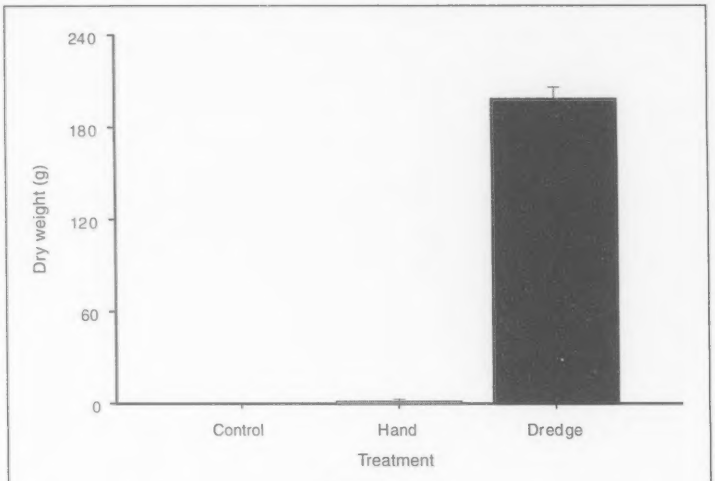

Figure 1

Mean (±1 SE) dry weight of seagrass displaced from control (undisturbed), hand-harvested, and dredged plots of seagrass during the 10 minutes during which the treatments were applied. n=3.

ful in removing both roots and shoots in their entirety (Peterson et al., 1983a). Shoots and roots, which were collected in a 3-mm nylon mesh bag, were dried at 60°C to constant weight to calculate total dry weight biomass of seagrass.

ANOVAs allowed us to test for a significant interaction between time (before versus after) and disturbance (dredge versus hand-harvest versus control) in the biomass of seagrass and recruit density of bay scallops (a basic BACI design; Green, 1979), indicative of an impact of harvest. The cause of any significant time × disturbance interactions was explored by using Student-Newman-Keul (SNK) tests. Prior to each analysis, Cochran's (1951) C-test was done to test for heterogeneity of variances. Where variances were heterogeneous, data were ln (x+1) transformed to remove heteroscedasticity at $\alpha = 0.05$.

Results

Of the two methods used to harvest adult scallops, hand harvesting had by far the greater efficiency in these shallow waters (ANOVA, P<0.0001). Over a period of 10 minutes, an average of 156 ±12 (1 SE) scallops within each 25 × 8 m plot was harvested by hand as compared to 26 ±1 scallops with the dredge.

The two methods of harvesting differed significantly in their impact on seagrass. Hand harvesting of scallops did not increase dislodgement of seagrass above the natural drift rate (Fig.1). Dredging, in contrast, resulted in 127 times the export of seagrass. This extraction did not, however, result in detectable reductions in biomass per unit of area of seagrass within dredged plots when sampled one month later. There was no significant temporal change in the biomass of seagrass in any of the three treatments from before to one month after harvesting (Table 1, Fig. 2).

Fewer than 2% of the estimated total number of juvenile scallops in a plot were directly removed by dredging and none was removed by hand-harvesting. Nevertheless, sampling one month after harvesting indicated depressed densities of juvenile bay scallops in dredged plots (Table 2; Fig. 3). This difference could not be attributed to natural change; small increases (16–55%) in numbers of juvenile bay scallops in the hand-harvested and control plots were documented over the same period (Fig. 3). A comparison of size-frequency histograms of juvenile bay scallops within each type of plot from before to after harvesting revealed that the decrease in juvenile scallop numbers in the dredged plots was primarily due to losses of scallops in the smallest size classes (<14 mm; Fig. 4). In the dredged plots, mean (±SE) size of juveniles (≤40 mm in shell height) increased from 17.04 ±0.83 in January to 20.43 ±0.76 in February. Over the same time period, mean size changed little in the control (16.09 ±0.85 to 16.75 ±0.75 mm) or in the hand-harvested (18.19 ±0.85 to 17.95 ±0.65 mm) plots.

Discussion

Previous research indicates that the implementation of certain gear restrictions on estuarine bivalve fisheries can minimize habitat destruction without sacrificing harvesting efficiency (Peterson et al., 1983b; Lenihan and Peterson, 2004). In our study, which successfully mimicked the efficiency of commercial dredging and

Table 1

BACI (Green, 1979) analysis of variance that tests for an impact of scallop harvesting on biomass of seagrass. Nine plots of seagrass were randomly assigned to three treatments: undisturbed control, hand-harvested, dredged. Biomass of seagrass was determined immediately before (Jan 2002) and one month after (Feb 2002) application of treatments to plots. $n = 5$.

Source	df	MS	F	P
Before versus after treatment	1	0.14	0.78	0.41
Treatment	2	0.35	0.81	0.49
Plot (treatment)	6	0.43	3.50	0.00
Before vs. after × treatment	2	0.26	1.41	0.31
Before vs. after × plot (treatment)	6	0.18	1.49	0.19
Residual	72	0.12		
Transformation	ln $(x+1)$			
Cochran's test	$C=0.16$ $(P>0.05)$			

hand-harvesting of bay scallops (see Burgess and Bianchi[3]), hand-harvesting yielded six times the bay scallop harvest obtained per unit of time by dredging, while reducing deleterious environmental effects. Hand-harvestikng did not result in uprooting of seagrass or displacing juvenile bay scallops, whereas dredging caused significant damage to seagrass. Ten minutes of dredging resulted in an average dry weight loss of 200 g of seagrass per plot—9 % of the estimated biomass of seagrass present prior to harvest. Despite this sizable removal of seagrass biomass, a persistent impact of dredging on seagrass biomass was not detected one month later. To the contrary, a 39% increase in seagrass biomass was seen across the dredged plots that was not replicated in the control plots. This result indicated that dredging had only a short-term negative impact on seagrass shoots (the necessary production of new leaves) and instead appeared to stimulate new production during the winter period that was more than sufficient to replace dredging damage.

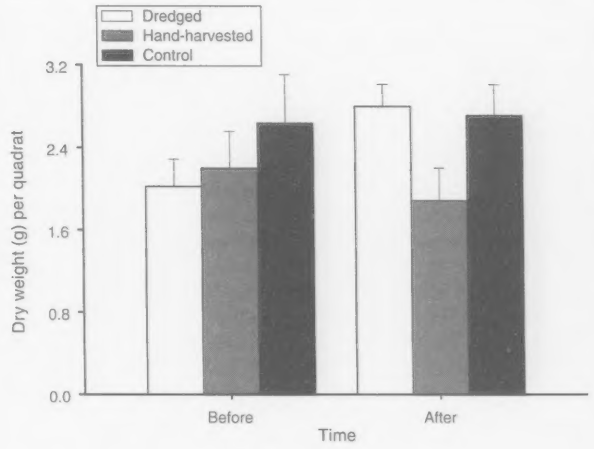

Figure 2

Mean (±1 SE) dry weight of seagrass per 0.25-m^2 quadrat in control (undisturbed), hand-harvested, and dredged plots immediately before and one month after the 10-minute treatments were applied. n=15.

Despite the rapid recovery of seagrass from dredging injury, a sustained negative impact of dredging on the density of juvenile bay scallops within plots was detected over the one-month period of our study. In contrast to the small increases in juvenile scallop density that occurred in hand-harvested and control plots over the course of the study, mean density of juveniles in dredged plots declined from 1.37 ±0.33 (1 SE) to 0.89 ±0.23 per 0.5 m^2. This 40% reduction in juvenile scallops in dredged plots cannot be explained by the bycatch alone. Whereas total bycatch of juveniles was, on average, two scallops per dredged plot, the average reduction in the density of juvenile bay scallops was 0.5 per 0.5-m^2 quadrat or 200 per 200-m^2 plot.

Instead, the reduction in density of juvenile scallops in dredged plots is best explained by their migration after dredging injury to seagrass habitat into adjacent undisturbed control and hand-harvested plots. Abundances of juvenile bay scallops in hand-harvested and control plots increased over the one month of our study by an amount more than sufficient to compensate for losses of juveniles from dredged plots. These increases in abundances in control and hand-harvested plots cannot be attributed to the settlement of new recruits: fall recruitment of juvenile scallops to seagrass beds is typically completed by the end of December (Peterson et al., 1989), spring spawning does not commence until March (Peterson and Summerson, 1992), and scallops spawned during our experiment could not possibly have grown fast enough over one month to reach a size re-

Table 2

BACI analysis of variance testing for an impact of scallop harvesting on density of scallop recruits. Nine plots of seagrass were randomly assigned to three treatments: undisturbed control, hand-harvested, dredged. Density of scallop recruits was determined immediately before (Jan 2002) and one month after (Feb 2002) application of treatments to plots. n=9.

Source	df	MS	F	P
Before vs. after treatment	1	0.89	0.78	0.41
Treatment	2	5.57	2.74	0.14
Plot (treatment)	6	2.03	0.77	0.59
Before vs. after × treatment	2	4.57	4.01	0.08
Before vs. after × plot (treatment)	6	1.14	0.43	0.85
Residual	144			
Cochran's test	C = 0.13 (P>0.05)			
SNK tests	Before vs. after × treatment Before: control = hand-harvested = dredged After: control = hand-harvested > dredged			

tained by sieves (see Irlandi et al., 1999 for growth rates). Scallops colonizing hand-harvested and control plots were of the right size and of sufficient abundance to be those missing from dredged plots. The migration appears to have included active swimming because tidal currents were perpendicular to the direction of scallop movement.

Although juvenile scallops are largely sessile, our interpretation that juveniles migrate in response to dredging is consistent with field and laboratory observations of juvenile bay scallop behavior. During seasonal sloughing of eelgrass blades, juvenile bay scallops break away and re-establish byssal attachments to seagrass blades (Thayer et al., 1975). Mesocosm observations confirm that juveniles are capable of swimming distances of at least several meters when displaced (Bishop, personal observ.). Thus, our experimental restriction on dredging to small areas may have facilitated relocation of scallops to adjacent, undisturbed habitat, where they remained one month later even after seagrass had regrown in the dredged plots. In the case of the commercial fishery, however, juvenile scallops emigrating from disturbed habitat over the extensive fished areas would be far less likely to encounter undisturbed seagrass habitat for re-attachment. Indeed, transport to unfavorable unvegetated habitat where predation risk is enhanced would likely inflate mortality.

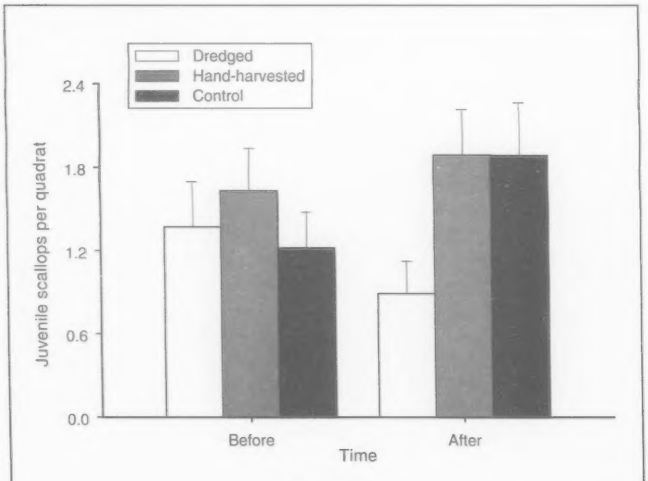

Figure 3

Mean (±1 SE) number of juvenile bay scallops (≤40 mm in shell height) per 0.5-m^2 quadrat in control (undisturbed), hand-harvested, and dredged plots immediately before and one month after the 10-minute treatments were applied. n=15.

In our study, juvenile scallops lost from the dredged plots came primarily from the smallest size classes. Small juvenile scallops are more susceptible to benthic predators that forage within seagrass beds than larger juveniles (Pohle et al., 1991). Because the foraging efficiency of some predators increases with decreasing biomass of seagrass (Prescott, 1990), a decrease in seagrass biomass, even for a period of weeks, would likely increase predation on juvenile scallops. Thus, small juveniles probably are increasing their chances of survival by emigrating away from depleted and into denser seagrass. Larger juveniles, in contrast, experience a partial size refuge from predators (e.g., Pohle et al., 1991), and thus have less incentive to emigrate.

This study considered the impact of only a single bay scallop-harvesting event on seagrass biomass and abundance of juvenile bay scallops within small experimental plots. Fishing disturbances are, however, typically chronic, occurring multiple times within a given season, and over large spatial scales.

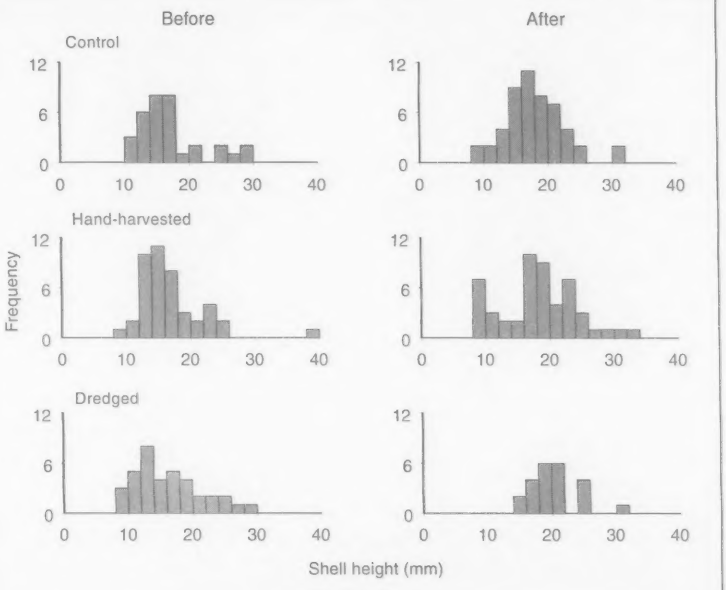

Figure 4

Size-frequency distribution of juvenile bay scallops (≤40 mm in shell height) collected from control, hand-harvested, and dredged plots immediately before and one month after the 10-minute treatments were applied.

In our study, just 10 minutes of dredging resulted in the removal of approximately 9% of the total biomass of seagrass in the experimental plot. Repeating this fishing disturbance over large spatial scales could, therefore, have substantial detrimental effects on seagrass habitat and, as an indirect result, the abundance of bay scallops that comprise the next generation. In addition, other habitat functions of seagrass are likely compromised until regrowth occurs. Peterson et al. (1987) demonstrated in this same system that a one-time reduction of 65% in seagrass biomass from gear disturbance during clam harvesting was not replaced over a subsequent 2-year period free of additional fishing.

The results of our study raise doubt about the sustainability of a bay scallop fishery in which the harvest method is dredging. Because this species, which lives only 12–24 months, is recruitment-limited (Peterson and Summerson, 1992; Peterson et al., 1996), reductions in densities of juvenile bay scallops by dredging will not only diminish that year's harvest but also presumably result in less spawning-stock biomass. Without restrictions on scallop dredging, impacts of dredging disturbance compounded across years may lead to the gradual collapse of the fishery. Re-imposing gear restrictions in shallow areas where hand harvest is practical may, therefore, pay big dividends. When use of the less destructive hand method carries little or no penalty of reduced fishing success, restricting scallop dredging from shallow SAV represents an appropriate ecosystem-based management choice (Botsford et al., 1997) that may sustain SAV habitat and restore a bay scallop fishery now in serious decline (Burgess and Bianchi[3]).

Acknowledgments

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Longline-caught blue shark (*Prionace glauca*): factors affecting the numbers available for live release*

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The blue shark (*Prionace glauca*) is an oceanic species that occurs in temperate and tropical waters around the globe (Robins and Ray, 1986). This species is a major bycatch of pelagic longline fleets that operate to supply the world's growing demand for tunas and swordfish (*Xiphias gladius*) (Stevens, 1992; Bailey et al., 1996; Francis, 1998; Francis et al., 2001; Macias and de la Serna, 2002); numerically, the blue shark is the top nontarget species captured by the U.S. longline pelagic Atlantic fleet (Beerkircher et al.[1]).

Ward et al. (2004) examined the effect of longline soak time (set duration) on the catch rate of several target and bycatch species, including the blue shark. However, they did not investigate the effects of fish size, set duration, and water temperature on shark survival, and, therefore, numbers potentially available for live release (Francis et al., 2001; Campana et al.[2]). Knowledge of such relationships may be of value: 1) for minimizing bycatch mortality on this and other highly vulnerable pelagic species through modification of fishing strategy; and 2) for blue shark stock assessments that are based on commercial longline catch data.

Materials and methods

Data analyses were conducted on a portion of the U.S. Atlantic Pelagic Observers Program (POP) database. The POP places trained observers aboard commercial fishing vessels to record detailed information about each fishing set, the catch and the bycatch that would not otherwise be collected. Recorded information includes individual fish size (measured or estimated) and disposition (alive or dead), surface water temperature (°C) at gear deployment and at haulback, and set location (latitude and longitude). The duration of each set (soak time, in hours) can be obtained because time at start of gear deployment and at end of gear retrieval is also recorded. In the present study, we restricted our analyses to observed sets made from 1992 to 2002 by U.S. flag vessels north of 35°N latitude (Fig. 1). This area includes much of the U.S. exclusive economic zone north of Chesapeake Bay but also includes waters overlying the Grand Banks. Data resulting from experimental fishing conducted from 2001 to 2004 over the Grand Banks area (i.e., north of 35°N latitude and west of 60°W longitude) were not included because they did not reflect typical fishing operations.

For analysis purposes, blue shark were placed in 25-cm fork length (FL) size classes and water temperatures (means) and set durations into 2°C and 2-hour intervals, respectively.

Size intervals were set at 25 cm FL to increase the number of observations in each size category and to reduce the bias that results from estimating lengths versus actually measuring them (e.g., observed increase in the frequency of the estimated lengths in 5- or 10-cm intervals). For each combination of size, temperature, set duration, season, and area (i.e., Grand Banks and U.S. Atlantic east coast), the proportion of blue shark released alive (P_{DA}) was calculated.

Only sharks explicitly recorded as "discarded alive" or "discarded dead" were used and only proportions derived from at least 20 observations (i.e., captured sharks) were analyzed. The influence of the fish size, water temperature, set duration, area, and season (and all possible interactions) on P_{DA} was assessed by using the linear model

$$P_i = \beta_0 + \beta_1 T_i + \beta 2\, D_i + \beta 3\, S_i + \beta 4\, L_i + \beta 5\, A_i + \epsilon_i,$$

where P_i = to the proportion of blue shark discarded alive;
T = the temperature;
D = set duration;
S = season;
L = length;
A = set area,
ϵ = the residual term of the i^{th} observation; and
$\beta_0 - \beta 5$ are model parameters.

Prior to regression, proportions were arcsine-transformed according to the methods of Sokal and Rohlf (1981). In

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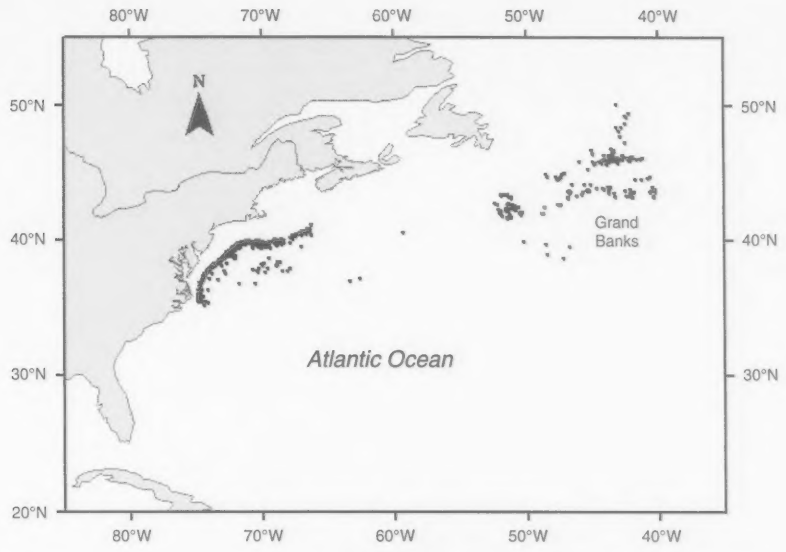

Figure 1

Locations of observed longline sets (1992–2002) recorded in the U.S. Pelagic Observers Program database and analyzed in the present study.

the event that a factor was found to be nonsignificant ($P>0.05$), it was removed and a regression was rerun until all highest order model terms were significant (Hocking, 1976; Draper and Smith, 1981). We assumed maturity (both sexes) occurred at 185 cm FL (Pratt, 1979). The average P_{DA} and the ratio of immature-to-mature individuals discarded in each 0.5-degree cell were estimated and plotted in order to visually examine the spatial distribution of these two variables.

Results

Data from 702 longline sets were used in analyses and resulted in size and condition (i.e., live or dead) information on 4290 individual blue shark. From these data, a total of 37 proportions (i.e., P_{DA} values) were calculated and used in regression analyses.

Most of the sets targeted swordfish (39%) or swordfish and tuna (36%), or unspecified tuna species (14%). Bigeye tuna and yellowfin tuna were the target of 8% and 3% of the sets, respectively. About 88% of the sets included in the analysis were characterized as "night sets" and the remaining were "day sets."

Overall, more blue shark were released alive (69%) than dead. Shark sizes, water temperatures, and set durations used in the multiple linear regression ranged from 75 to 300 cm FL (median=175 cm), 8 to 29°C (median=19°C), and 6 to 14 hours (median=12), respectively. About 68% of all released animals measured less than the size of sexual maturity (i.e., <185 cm FL).

Multiple linear regression indicated that no interaction terms were statistically significant and that only shark size and set duration had significant effects on P_{DA} ($r^2=0.86$, $n=37$, $P<0.00001$; Table 1). Plots of the observed proportions and the predicted response surface illustrate how the proportion of live releases increases with shark size and decreases with duration of set (Fig. 2, A and B). Whereas set duration has a moderate impact on the largest size classes, the proportion of live sharks <185 FL (i.e., immature stages) is considerably reduced even at relatively short set durations. For example, predicted P_{DA} for the smallest sharks (i.e., FL=75 cm) was 0.67 and 0.47 for set durations of 6 and 14 hours, respectively; for those animals measuring 250 cm FL, it was 0.94 and 0.80 for the same set durations. Maps of mean P_{DA} values and of the proportion of immature sharks caught indicated conspicuous differences off the U.S. east coast versus over the Grand Banks (Fig. 3, A and B). Specifically, the proportion of live releases

Table 1

Regression coefficients and associated standard error values (SE) for the estimation of proportion of blue shark released alive (P_{DA}) ($n=37$), where β_0 corresponds to the intercept, and β_1 and β_2 are coefficients associated with blue shark fork length and set duration, respectively.

Parameters	Estimate	SE	$P>\|t\|$
β_0	0.967	0.0500	<0.0001
β_1	0.0021	0.0002	<0.0001
β_2	−0.0269	0.0037	<0.0001

tended to be lower over the Grand Banks than off the U.S. east coast and the mean ratio of immature blue shark tended to be higher.

Discussion

Our results indicate that blue shark tolerance to the stresses associated with longline capture decreases with animal size at levels that vary with set duration. These results are consistent with the findings of Neilson et al. (1989) and Milliken et al. (1999) who observed greater discard mortality among the smallest sizes classes of longline-caught Atlantic halibut (*Hippoglossus hippoglossus*) and cod (*Gadus morhua*), respectively. In our study, set duration represented the maximum possible time a given fish was "on-hook," and thus was only the coarsest of measures of the magnitude and duration of stress experienced by hooked fishes. Nevertheless, this crude measure appears to have captured enough of the cumulative stress effects on fish survival to emerge as a significant factor. In contrast, water temperature did not emerge as important in our analysis. However, we suspect this resulted because surface water temperatures (the only temperature measurements available) are poor indicators of the levels and changes in temperature actually experienced by captured sharks. Presumably, better predictions of condition at boat-side (and thus live discard quantities) could be made with knowledge of time-on-hook, depth, and temperature of capture, rate of gear retrieval, sea conditions, etc. Unfortunately, many of the measurements that are likely most relevant to recording shark condition at boat-side can only be made by distributing and retrieving large quantities of electronic instruments (i.e., temperature-depth recorders and hook-timers, see Boggs, 1992) near the hooks, and for each set. Such an approach is not only costly, but also difficult to implement without a research team dedicated for this purpose. Similarly, only by directed research can questions of postrelease mortality be addressed. Clearly, the proportions of living blue shark considered in our study are minimum estimates of fishing impacts because they do not account for delayed mortality of individuals released injured or otherwise impaired. For gauging postrelease mortality of longline-caught blue shark, tagging studies are warranted (Neilson et al., 1989; Kohler et al., 2002).

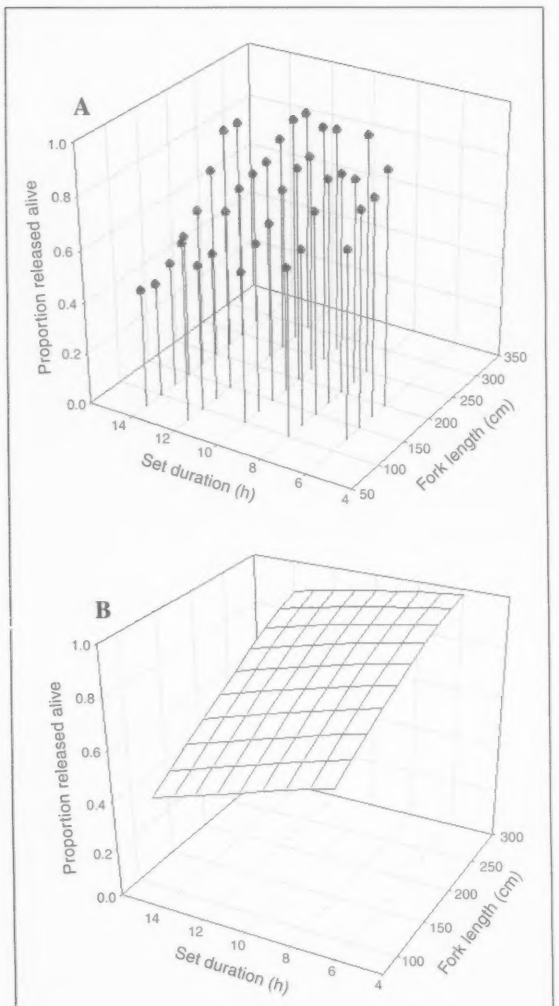

Figure 2

(**A**) Observed proportions of blue shark discarded alive (n=37) for each fork-length set duration combination; and (**B**) predicted response surface.

Evident in the maps is that the proportion of blue sharks available for live release was not homogeneous throughout the spatial range examined. Overall the proportion of blue shark released alive was higher (0.78) along the U.S. Atlantic east coast and decreased over the Grand Banks (0.67) (Fig. 3A). The maps also indicated that overall the proportion of immature blue sharks was highest over the Grand Banks (0.93) compared to the U.S. Atlantic east coast (0.63) (Fig. 3B). In their examination of U.S. Atlantic east coast longline catches south of the present study (i.e., between 35° and 22°N latitude), Beerkircher et al. (2004) found that 0.87 of blue shark caught were alive at boat-side. It seems likely, therefore, that contributing to the relatively higher survival observed by Beerkircher et al. (2004) was that only about half of the blue shark in their analysis were immature (as inferred from size). Blue shark interactions over the Grand Banks deserve special attention because most individuals discarded by the U.S. pelagic longline fleet are captured in that area. In 2002, for example, two thirds of the estimated 4335 blue shark mortalities attributed to U.S. Atlantic pelagic longline fleet were captured in this area (Diaz, unpubl. data[3]).

[3] Diaz, G. A. 2005. NMFS Pelagic longline logbook program. NMFS/SEFSC Miami, FL 33149.

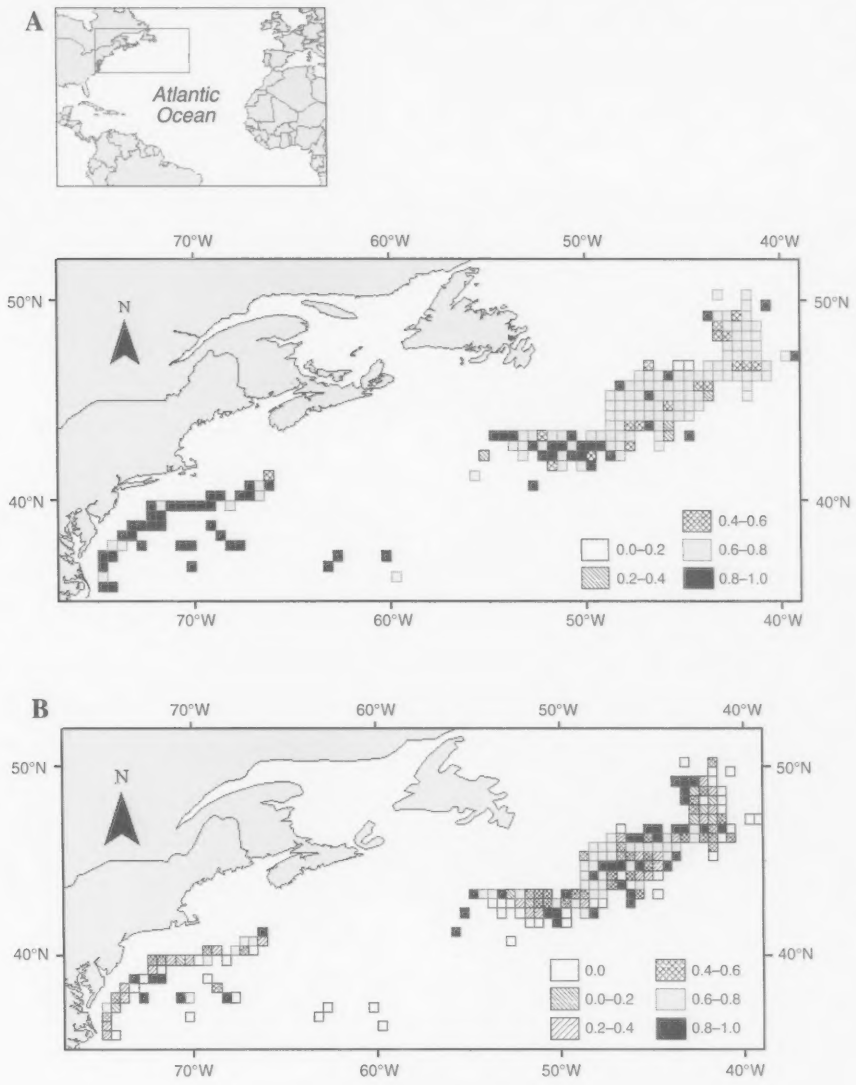

Figure 3

(**A**) Average proportion of blue shark released alive and (**B**) average proportion of immature blue shark released in pelagic longline sets. Proportions were estimated for 0.5-degree cells where at least one longline set was deployed in the period 1992–2002.

Ward et al. (2004) modeled the effect of set duration on pelagic longline catches and found that blue shark catch rates increased with set duration. According to our results, the increase in set durations also leads to increases in the number retrieved dead. In concept, a possible management measure to achieve reductions in blue shark mortality may include shortening longline set durations. However, a regulation of this nature would be difficult to implement (let alone enforce) because swordfish catch rates are also lowered when set durations are shortened (Ward et al., 2004) and therefore result in negative economic impacts that would likely be unacceptable to the industry.

Results of this analysis also have implications for blue shark stock assessment. Stock assessments based on longline fisheries data often use a hook selectivity function of a logistic form, whereby hook retention is 100% for fish larger than a certain size. In the particu-

lar case of blue shark, where most individuals caught are released (dead or alive), fishing mortality is best estimated from the number of animals released dead, rather than from all animals caught. Because larger animals have a higher probability of being released alive, a logistic selectivity function without size or age survival adjustment, could lead to overestimation of impacts on the stock. Thus, a dome-shaped selectivity function that incorporates the size-based survival information presented in the present study may represent an improvement over current techniques.

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Length correction for larval and early-juvenile Atlantic menhaden (*Brevoortia tyrannus*) after preservation in alcohol

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Body length measurement is an important part of growth, condition, and mortality analyses of larval and juvenile fish. If the measurements are not accurate (i.e., do not reflect real fish length), results of subsequent analyses may be affected considerably (McGurk, 1985; Fey, 1999; Porter et al., 2001). The primary cause of error in fish length measurement is shrinkage related to collection and preservation (Theilacker, 1980; Hay, 1981; Butler, 1992; Fey, 1999). The magnitude of shrinkage depends on many factors, namely the duration and speed of the collection tow, abundance of other planktonic organisms in the sample (Theilacker, 1980; Hay, 1981; Jennings, 1991), the type and strength of the preservative (Hay, 1982), and the species of fish (Jennings, 1991; Fey, 1999). Further, fish size affects shrinkage (Fowler and Smith, 1983; Fey, 1999, 2001), indicating that live length should be modeled as a function of preserved length (Pepin et al., 1998; Fey, 1999).

The goal of this study was to analyze the shrinkage of late-larval and early-juvenile Atlantic menhaden (*Brevoortia tyrannus*) during preservation in 95% alcohol. A length correction formula is presented that allows live standard length to be calculated from preserved standard length.

Materials and methods

Larval and early juvenile Atlantic menhaden were collected on three different occasions during January–March 2003 with a neuston net (2-m^2 opening and 947-μm mesh) deployed for 2-minute durations from a bridge to Pivers Island, located about 2 km inside Beaufort Inlet, North Carolina. Samples were placed in a cooler and transported to the laboratory. Live Atlantic menhaden larvae were sorted from the samples (n=100) and their standard lengths (SL) were measured to the nearest 0.01 mm with a caliper. All specimens (19.1–31.4 mm SL) were placed in individual vials filled with 95% ethyl alcohol. The fish were remeasured 3, 20, and 90 days after preservation.

Repeated measures ANOVA and Tukey HSD tests were used to analyze the significance of length changes during 90 days of preservation. The preserved length after 90 days was than compared with live length to test whether a single correction factor is appropriate for a calculation of live length (t-test analysis for the slope difference from one). Additionally, the precision of measurements was evaluated by two replicate measurements of all larvae three days after preservation. Linear regression analysis was then used to describe the relationship between the two length measurements. The possible deviation of intercept from zero and slope from one was estimated (t-test) to test for the possible significant differences between the two measurements.

Results

Time in preservative had a significant effect on measured length of Atlantic menhaden larvae (repeated measures ANOVA, P<0.0001). Fish were significantly larger prior to preservation compared to three days after preservation (Tukey HSD, P<0.001) and significantly larger three days after preservation compared to 20 and 90 days after preservation (Fig. 1) (Tukey HSD, P<0.001). When shrinkage is described as a relative value, the change in length that occurred during the first three days of preservation was 3.62%. Length decreased by an average of 0.22% during the following 17 days and by 0.073% during the remaining 70 days.

Although smaller fish shrank proportionally more than the larger ones (t-test for H_0: slope=0, P<0.001) (Fig. 2A), no size effect was observed when shrinkage was analyzed as absolute length (regression slope= 0.996, SE=0.008; H_0: slope=1; t-test of regression slope, P=0.605). However, the y-intercept of the regression of preserved length at 90 days on live length was significantly different from zero (regression intercept=1.17; SE=0.21; H_0: y-intercept=0; t-test of regression intercept, P<0.001) (Fig. 2B). Therefore, the significantly different from zero intercept can be used as a correction factor (i.e., $SL_{fresh}=SL_{preserved}+1.17$ mm). The shrinkage magnitude observed by Maillet and Checkley (1991) was compared to the results derived in our study (Fig 2B). Their formula indicated shrinkage of about 2% compared to approximately 4% in our study.

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The two readings performed to estimate the measurement error were not statistically different as indicated by the parameters of the regression line fitted to the first measurement versus second measurement data (SL_1=0.992 SL_2+0.21, r^2=0.998). The slope was not statistically different from one (regression slope=0.992, SE=0.005; H_0: slope=1; t-test of regression slope, P=0.106), and the intercept was not statistically different from zero (regression intercept=0.21; SE=0.12; H_0: y-intercept=0; t-test of regression intercept, P=0.418). Measurement precision, the absolute values of the difference between the two series of length measurements of the same specimens averaged 0.12 mm (SD=0.09), which corresponded to an average of 0.47% of length (SD=0.35). Thus, the error associated with measurement is an order of magnitude less than the change in length due to shrinkage within the first three days of preservation. Changes in length during following 87 days were below measurement error.

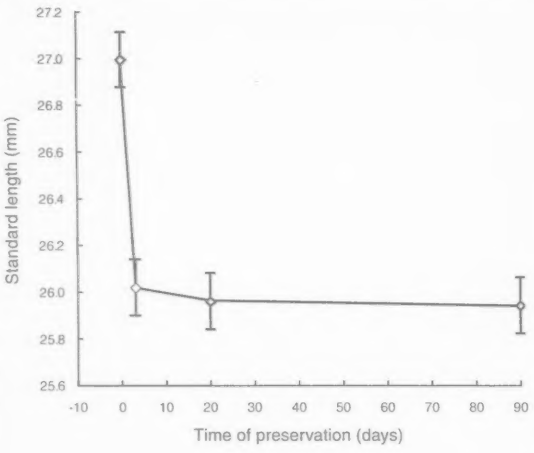

Figure 1

Change in standard length of Atlantic menhaden (*Brevoortia tyrannus*) (n=100) during 90 days of preservation in 95% alcohol. Mean values and standard error of length measurements obtained from repeated measurements of 100 fish.

Discussion

This research on late-larval and early-juvenile Atlantic menhaden shrinkage is the first for this species. Maillet and Checkley (1991) used a shrinkage correction formula (cited as unpubl. data) in their study on larval menhaden growth but did not provide additional information (e.g., range of fish sizes) to accompany their formula. Their correction formula differs from ours, and the discrepancy may be related to differences in experimental procedure and different developmental stages. In the present study live fish were used, but in Maillet and Checkley's study (1991) it was not indicated whether larvae were alive or dead prior to preservation. Further Maillet and Checkley (1991) examined larval menhaden (17–24.5 mm SL), whereas we examined late-larval to early-juvenile menhaden (19.1–31.4 mm SL).

The shrinkage of larval and early-juvenile Atlantic menhaden after the first three days of preservation was significant, but small in magnitude. Beyond 20 days of preservation significant additional shrinkage did not occur. In fact, the length changes after day 3 were below the estimated measurement

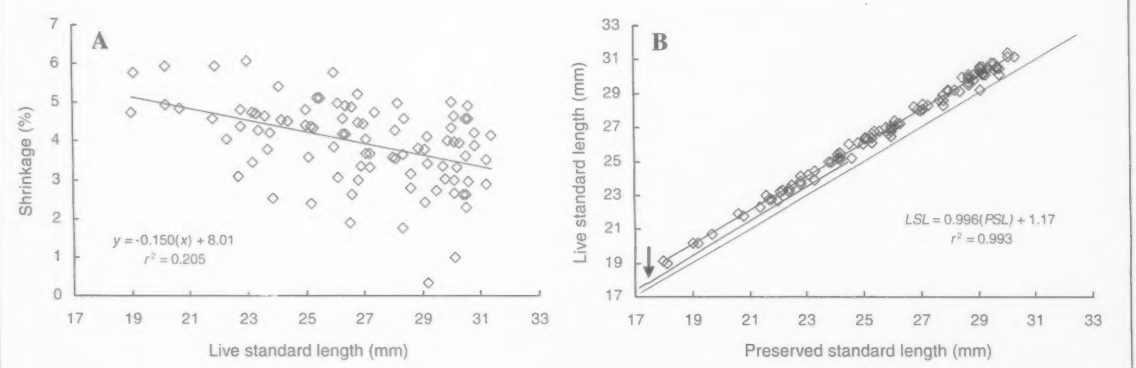

Figure 2

Length changes of Atlantic menhaden (*Brevoortia tyrannus*) during preservation for 90 days in 95% alcohol (n=100). (**A**) The relationship between live standard length (LSL) and relative (%) shrinkage magnitude; (**B**) the relationship between live and preserved standard lengths described with linear regression. The solid line indicates the 1:1 ratio. The arrow points to the correction curve obtained from Maillet and Checkley (1991): $SL_{live}=0.978(SL)e^{1.285e^{-0.578(SL)}}$.

error. Additionally, decreasing shrinkage as a function of increasing fish length was present when relative (%) shrinkage was analyzed. Similar results with regard to time and fish size effect were previously reported for other fish species preserved with formalin and alcohol (see Fey, 1999, for overview).

The effect of shrinkage on growth rate analysis was described by Fey (1999) for larval sprat. If growth rate is estimated by using a regression of length at age, the influence of shrinkage on growth estimates depends on the absolute value of length changes (i.e., expressed in mm) among small and large fish, and the error may be as high as 0.07 mm/d. However, if the absolute values of length decrease equally across fish lengths, even large shrinkage (on average) may have no effect on the results of growth rate analysis. In addition to length at age analysis, average growth rate (mm/d) may be calculated for individual fish. The potential error in growth estimates will then be directly proportional to both the relative and absolute magnitude of shrinkage. This potential bias in growth-rate calculations described by Fey (1999) for sprat emphasizes the importance of correcting for preservation. Although the relationship between otolith size and fish size may be used for length correction (Leak, 1986; Radtke, 1989), Fey (1999) showed that greater accuracy is provided when a fresh length–preserved length relationship is used. However, such a relationship may be supplemented by additional measurements (i.e., body depth and otolith size) to improve the accuracy of the correction model (Porter et al., 2001). In the current study, absolute changes in length (expressed in mm) of alcohol-preserved menhaden were not dependent on fish size and therefore a single correction factor was sufficient for a calculation of live length. The length correction factor provided in our study will benefit future studies on the ecology of early life stages of menhaden, similar to that conducted by Warlen et al. (2002), where preserved length measurements were used.

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Comparison of average larval fish vertical distributions among species exhibiting different transport pathways on the southeast United States continental shelf

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Water currents are vertically structured in many marine systems and as a result, vertical movements by fish larvae and zooplankton affect horizontal transport (Power, 1984). In estuaries, the vertical movements of larvae with tidal periods can result in their retention or ingress (Fortier and Leggett, 1983; Rijnsdorp et al., 1985; Cronin and Forward, 1986; Forward et al., 1999). On the continental shelf, the vertical movements of organisms interact daily and ontogenetically with depth-varying currents to affect horizontal transport (Pillar et al., 1989; Barange and Pillar, 1992; Cowen et al., 1993, 2000; Batchelder et al., 2002).

A suite of fish species, which use estuaries during the juvenile stage, spawn during winter on the mid- and outer continental shelf of the southeast United States (Fig. 1A): *Brevoortia tyrannus* (Atlantic menhaden), *Leiostomus xanthurus* (spot), *Micropogonias undulatus* (Atlantic croaker), *Paralichthys albiguta* (Gulf flounder), *P. dentatus* (summer flounder), and *P. lethostigma* (southern flounder). Vertically structured flow is a major part of proposed larval transport mechanisms for these species from offshore spawning areas to estuarine nursery habitats (Govoni and Pietrafesa, 1994; Hare et al., 1999). *Brevoortia tyrannus*, however, is found higher in the water column on average than the other species that use estuaries during their juvenile stage (Miller et al., 1984; Govoni and Pietrafesa, 1994; Govoni and Hoss, 2001). Further, larvae of *B. tyrannus* apparently exhibit a difference in horizontal transport compared to other winter-spawning species that use estuarine habitats as juveniles; *B. tyrannus* larvae spawned on the southeast U.S. shelf may be transported to estuarine nursery habitats along the northeast U.S. shelf (Warlen et al., 2002). The effects of differences in vertical larval distribution on cross-shelf larval transport are unknown, and the transport pathways from shelf spawning areas to estuarine nursery areas remain unclear.

Other species also spawn during winter on the southeast United States continental shelf. Some species settle to benthic habitats on the shelf (e.g., *Etropus cyclosquamus* [shelf flounder], *E. microstomus* [smallmouth flounder], and *E. rimosus* [grayflounder], Leslie and Stewart, 1986) or remain on the shelf in pelagic habitats (e.g., *Etrumeus teres* [round herring], Crawford, 1981; Schwartz, 1989). However, some species are regularly advected offshore, entrained into the Gulf Stream, and exported northwards (e.g., *Bothus* spp. [peacock, eyed, and spotted flounders], *Peprilus triacanthus* [butterfish], *Syacium papillosum* [dusky flounder], *Xyrichtys novacula* [pearly razorfish]; Hare and Cowen, 1991; Cowen et al., 1993; Rotunno and Cowen, 1997; Grothues and Cowen, 1999).

The purpose of our study was to examine associations between average larval fish vertical distributions and general larval transport pathways on the southeast United States continental shelf during winter. Our goal was to determine if larval vertical distributions differed among species that exhibit different outcomes of larval transport: export from the local shelf, arrival at local estuaries, and retention on the shelf. Our approach, however, was unconventional. Rather than couple detailed descriptions of the flow field with detailed describitions of larval vertical distributions (including diel variation), we chose to compare average vertical distributions among species that exhibit overall differences in larval transport. Vertical distribution data were collected in three separate years, over periods of time ranging from 24 to 96 hours. If average larval vertical distributions are different among species, and these differences occur consistently among the various sampling times and in concordance with the general outcome of transport, then we conclude that larval vertical distributions are an important part of larval transport on the southeast U.S. shelf.

Our specific objectives were twofold: 1) to test the null hypothesis that there are no differences in larval fish vertical distributions between species, and 2) to evaluate significant differences in larval depth distribution in relation to the *a priori* classification of the outcome of transport. Vertically discrete data from six sampling times were analyzed, and owing to differences in protocols among sampling times, comparisons of larval vertical distributions were made within sampling times only. The results of these comparisons were then combined to evaluate whether there were consistent differences in larval vertical distributions among sampling times related to the outcome of larval transport.

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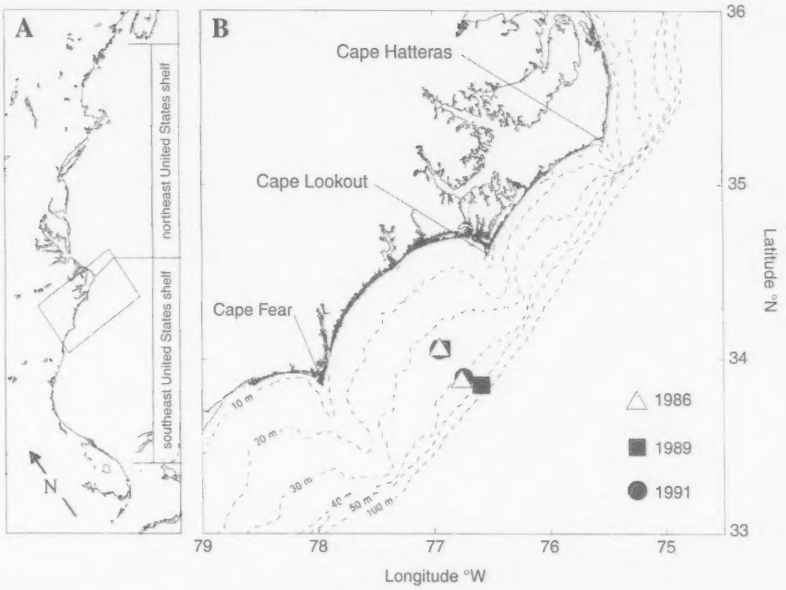

Figure 1

(**A**) Map of the east coast of the United States rotated 18° counter-clockwise. The spatial extent of the northeast and southeast United States continental shelves is indicated by each rectangle. The area of panel B is shown as a trapezoid. (**B**) The northern portion of the southeast United States continental shelf showing the coastline, the 10-m, 20-m, 30-m 40-m, 50-m, and 100-m isobaths. The three prominent capes are identified and locations of stations sampled in this study are shown.

Material and methods

Data collection

Larval fish were collected every six hours (0600, 1200, 1800, and 2400) at an offshore and an inshore station during three winters: 21–26 February 1986, 26 January–1 February 1989, and 5–7 February 1991 (Fig. 1B). Offshore stations were located on approximately the 50-m isobath, and inshore stations were located on approximately the 35-m isobath. In 1986, offshore and onshore stations were occupied for 102 and 48 h, respectively. Collections were taken horizontally at 1, 18, and 32 m at the offshore station and 1, 13, and 25 m at the inshore station with a 60-cm opening-closing bongo net (Weibe and Benfield, 2003) with 333-μm mesh and a 1-m^2 Tucker trawl (Weibe and Benfield, 2003) with 202-μm mesh. In 1989, offshore and inshore stations were occupied for 78 and 72 hours, respectively. Collections were taken horizontally at 1, 22, and 45 m at the offshore station and 1, 13, and 30 m at the inshore station with a 1-m^2 Tucker trawl with 333-μm mesh. In 1991, offshore and inshore stations were occupied for 24 and 30 h, respectively. Collections were made with 1-m^2 MOCNESS (Wiebe et al., 1976) with 333-μm mesh. Oblique samples were collected within 5-m intervals from 35 m to the surface at the offshore station and from 30 m to the surface at the inshore station. The mid-point of each depth stratum was used as the depth of the collection. In 1986 and 1989, volume of water filtered was measured with a flowmeter (General Oceanics model 2030, Miami, FL) with a standard rotor. In 1991, volume filtered was measured with a flowmeter provided with the MOCNESS (BESS, Falmouth, MA).

Larval fish were sorted from collections and identified to the lowest taxon possible. The larvae of selected taxa were counted: *Bothus* spp., *Etropus* spp. (not including *E. crossotus*), *E. teres*, *Paralichthys* spp., *P. triacanthus*, *S. papillosum* and *X. novacula*. Counts of *B. tyrannus*, *L. xanthurus*, and *M. undulatus* were obtained from Govoni and Pietrafesa (1994) and Govoni and Spach (1999). Larval concentrations were calculated for each depth stratum (number of larvae/100 m^3).

Comparisons of larval vertical distributions

Center of mass calculations are frequently used for comparison of fish larval depth distributions (e.g., Brodeur and Rugen, 1994), but Pearre (1979) raised valid criticisms of this approach; for example a uniform distribution still has a mean depth. To obviate these criticisms, larval depth distributions of each taxon were compared

by using a test of independence (Pearson chi-square, Sokal and Rohlf, 1981; McCleave et al. 1987). Depth distributions were averaged over each station. Comparisons were then made between all pairs of taxa within a station, and a Bonferoni correction was applied to assess the significance of the tests of independence. Comparisions were not made between stations, because sampling methods varied and depth distributions were not directly comparable. The following null hypothesis was evaluated: during each station occupation, average larval depth distributions were independent of species. Column and row variables were species and depth strata; cell values were the average proportion of the larvae captured in a depth stratum at a station. Comparisons of center of mass were also made and the results were very similar to the results of the test of independence reported in the present study.

The calculation of average proportion was made in two steps. First, the proportion of larvae (P) collected in each depth stratum (d) at each sampling time (i) during each station occupation (j) was calculated:

$$P_{dij} = \frac{C_{dij}}{\sum_{d} C_{dij}},$$

where C = larval concentration 100/m^3.

Then the average proportion of larvae ($\bar{P}$) for each depth stratum (d) was calculated for each station (j):

$$\bar{P}_{dj} = \frac{\sum_{i} P_{dij}}{n_{ij}},$$

where n_{ij} = the number of sampling times (i) during station occupation (j).

Because the significance of a test of independence depends, in part, on the magnitude of the cell values (i.e., sample sizes), average larval concentration of each species during each station occupation (number of larvae/100 m^3) was used as a weighting factor. The average proportion of larvae at depth during a station occupation ($\bar{P}_{dj}$) was multiplied by the weighting factor to derive the cell values for use in the test of independence. The weighting factor approximated the number of fish larvae collected, and incorporated the effect of variability in sampling volume.

Values of the standardized residuals, which are a result of the test of independence, were used to classify significant differences in depth distribution as follows: species A shallower (<) than species B, species A deeper (>) than species B, and species A distributed differently (< or >) than species B. This last category was assigned when one species was not clearly deeper or shallower than the other species, yet its depth distributions were significantly different.

To evaluate whether larval fish vertical distributions were associated with larval transport, the results of the individual species comparisons were pooled across station by the *a priori* assigned outcome of transport. The number of significant differences found between species were then compared to the number of significant differences expected with a 5% error rate by using the G-statistic (Sokal and Rohlf 1981). For example, in a comparison of *B. tyrannus* to exported species, five pairwise comparisons of larval depth distributions were found to be significantly different and 12 were not significantly different. At α=0.05, one significant and 16 nonsignificant differences are expected. The G-statistic demonstrates that more significant differences were found between *B. tyrannus* and exported species than expected by chance. The classifications of significant depth differences (shallower, deeper, different) were then examined to determine the relation between larval vertical distributions and the general outcome of larval transport.

Results

Comparison of larval vertical distributions indicated that *B. tyrannus* often had the shallowest larval vertical distribution. There were more significant differences than expected by chance between the vertical distributions of *B. tyrannus* and exported, estuarine, and shelf-resident taxa (Table 1). For all significant differences, the standard deviates from the test of independence indicated that *B. tyrannus* were found in shallower water than were other taxa (Appendix 1).

Exported taxa generally were higher in the water column than estuarine and shelf-resident taxa. There were more significant differences than expected by chance between the vertical distributions of exported taxa and estuarine and shelf-resident taxa (Table 1). Further, 9 of 12 significant differences between exported and estuarine taxa indicated that exported taxa were found in shallower water; 8 of 11 significant differences between exported and shelf resident taxa indicated that exported taxa were found in shallower water (Appendix 1).

The vertical distributions of estuarine and shelf-resident taxa were different more often than expected by chance, but taxa of neither group were consistently found in shallower water (Table 1). Significant differences in larval vertical distributions were distributed evenly among the three classifications of the direction of difference (n=4 shallower; n=2 deeper; n=5 different) (Appendix 1).

Discussion

The results indicate an overall hierarchy of larval vertical distributions; *B. tyrannus* was found in shallower water than were exported taxa, and exported taxa were shallower than estuarine and shelf-resident taxa. Although this general pattern emerged, considerable variability in larval vertical distributions was observed, which is a common result of many studies (e.g., Boehlert

Table 1

Summary of the pairwise comparisons of larval depth distributions between species classified by the *a priori* outcome of transport. In each table cell, the number to the left is the number of significant pairwise differences, the number to the right is the total number of comparisons across the six station occupations, and the number in parentheses is the *G*-statistic for evaluating the null hypothesis that the number of observed differences is as expected with a 5% error rate. The critical value at α=0.05 is 5.99 and significant values are indicated in bold. Values greater than 5.99 indicate that there are more significant differences between species than expected by chance. Exported taxa are *Bothus* spp., *Peprilus triacanthus*, *Syacium papillosum*, *Xyrichtys novacula*. Estuarine taxa include *Leiostomus xanthurus*, *Micropogonias undulatus*, and *Paralichthys* spp. Shelf resident taxa include *Etropus* spp. and *Etrumeus teres*.

		A priori classification of the outcome of transport		
	Brevoortia tyrannus	Exported	Estuarine	Shelf resident
Exported	5 / 17 (**10.29**)	2 / 17 (1.17)		
Estuarine	12 / 15 (**55.35**)	12 / 43 (**23.88**)	5 / 13 (**12.96**)	
Shelf resident	9 / 12 (**39.11**)	11 / 34 (**25.09**)	11 / 30 (**27.96**)	2 / 6 (4.39)

and Mundy, 1994; Brodeur and Rugen, 1994). Variability in larval fish vertical distributions (and zooplankton) is related to processes that influence water column mixing (e.g., Heath et al., 1988; Incze et al., 2001) and to species-specific responses to diel cycles and gradients in turbulence, temperature, and salinity (DeVries et al. 1995; Olla et al., 1996; Gray and Kingsford, 2003). The approach used in the present study was to average over shorter-scale variability (hours) in larval vertical distributions to examine longer-time-scale patterns (days) in larval vertical distributions.

Average larval vertical distributions of exported, estuarine-dependent, and shelf-resident taxa and the implied outcomes of their larval transport are consistent with the results of physical oceanographic models and observations of shelf circulation in the southeast United States continental shelf. The model of Janowitz and Pietrafesa (1980) (see also Miller et al., 1984) indicated a three-layered, cross-shelf flow during winter: surface and near-bottom offshore flow, and intermediate onshore flow. Similarly, the model of Werner et al. (1999) indicated a two-layered, cross-shelf flow during winter: an offshore flow near the surface and onshore flow throughout the rest of the water column. Surface flow in the study area during winter is typically offshore (Govoni and Pietrafesa, 1994). On the inner and middle shelf (water depths <40 m), average bottom flow is onshore; on the outer shelf (water depth 40–75 m), average intermediate flow is onshore, whereas bottom flow is offshore (Fig. 5b in Lee et al., 1989). Modeled and observed flow fields may indicate that larvae in the surface water will move offshore (exported taxa), where the probability of entrainment into the Gulf Stream is higher. Larvae that are in the middle or lower portion of the water column will move onshore (i.e., estuarine-dependent and shelf-resident taxa). Thus, the average larval vertical distributions, the general outcome of larval transport, and the generalized observed and modeled vertical flow fields are consistent.

Differences between vertical distributions of larval *B. tyrannus* and the other estuarine-dependent taxa (Fig. 2; see also Govoni and Pietrafesa, 1994) imply differences in cross-shelf transport. There are several possibilities, none mutually exclusive. 1) Onshore transport of larval *B. tyrannus* occurs with northeast wind events and onshore transport of other estuarine-dependent larvae occurs with southwest or northwest wind events. This possibility is supported by the model simulations of Hare et al. (1999). 2) Cross-shelf transport of *B. tyrannus* larvae occurs in surface Gulf Stream intrusions (Checkley et al., 1988; Stegmann and Yoder, 1996), whereas cross-shelf transport of other estuarine-dependent larvae occurs by wind-driven mechanisms. This possibility has not been adequately evaluated. 3) All estuarine-dependent larvae are transported across the shelf by the same mechanisms, but the rate of their transport differs. For example, southwest wind events cause onshore transport rates to be greater for the other estuarine-dependent taxa because *B. tyrannus* larvae spend less time in the intermediate portion of the water column. This possibility is also supported by Hare et al. (1999), who found that in modeled larval vertical distributions, the outcome of larval transport was modified by circulation. From these alternative hypotheses, it is clear that our understanding of the cross-shelf transport of larval fishes remains incomplete and that the effective physical and biological mechanisms are complex.

One approach to resolving the affect of vertical distribution on cross-shelf larval transport is to develop a specific hypothesis regarding supply of larvae to inlets that is based on the above possibilities and then to test these hypotheses using the long time-series of larval ingress collected at Beaufort Inlet (see Warlen, 1994). Three alternative patterns in ingress, based on the three possibilities presented above, could be evaluated by using ingress data collected at Beaufort Inlet: 1) ingress of *B. tyrannus* occurs during northeast winds, and

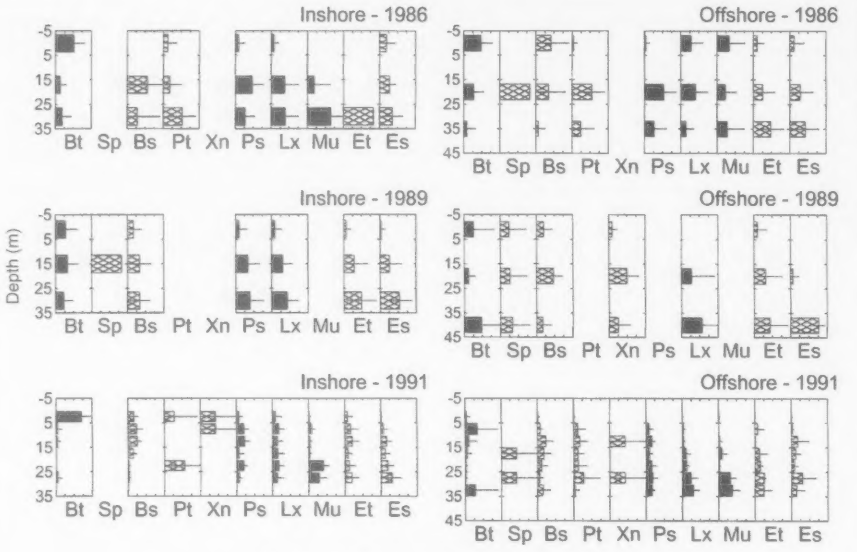

Figure 2

Mean proportions of larvae sampled at depths at six stations on the southeast United States shelf. Error bars indicate standard deviation of mean proportions calculated by using all the samples collected at a station. The *x*-axis of all panels is the same and ranges from 0 to 1.2. The species indicated in each figure is denoted by a two letter code (Bt=*Brevoortia tyrannus*, Sp=*Syacium papillosum*, Bs=*Bothus* spp., Pt=*Peprilus triacanthus*, Xn=*Xyrichtys novacula*, Ps=*Paralichthys* spp., Lx =*Leiostomus xanthurus*, Mu=*Micropogonias undulatus*, Et=*Etrumeus teres*, and Es=*Etropus* spp.). Species are grouped by an *a priori* assignment of their general outcome of transport.

the ingress of other species occurs during northwest, west, and southwest winds; 2) ingress of *B. tyrannus* is not related to wind, and ingress of the other species is related to northwest, west, and southwest winds; 3) and ingress of all estuarine-dependent species occurs during similar wind forcing. Other studies have established similar *a priori* predictions for relations between wind forcing and ingress, yet results have been equivocal (e.g., Blanton et al., 1995). One explanation is that cross-shelf larval transport and larval ingress occur through multiple steps (Boehlert and Mundy, 1988; Hettler and Hare, 1998), effectively decoupling wind-driven, cross-shelf larval transport from larval ingress.

Similarities in vertical distributions of larval *B. tyrannus* and exported larval taxa indicate that a greater proportion of *B. tyrannus* larvae may be entrained into the Gulf Stream than larvae of other species that use southeast estuaries as juvenile nurseries. Once entrained into the Gulf Stream, larvae are transported northeastward and they either continue to move in the Gulf Stream or are returned to the shelf edge north of Cape Hatteras by warm-core ring streamers or in discharges of Gulf Stream water (Hare and Cowen 1991, 1996; Churchill et al., 1993; Cowen et al., 1993; Hare et al., 2002). Govoni and Spach (1999) reported offshore exchange of *B. tyrannus* larvae into the Gulf Stream, and Warlen et al. (2002) concluded that some *B. tyrannus* larvae spawned south of Cape Hatteras do enter estuaries north of Cape Hatteras in the spring. The mechanisms of northward transport of *B. tyrannus* have yet to be studied, but transport to the northeast United States shelf edge by the same mechanisms as those that drive exported taxa is possible.

In marine systems, larval fish interact with vertically structured flow with vertical motions and thereby affect their horizontal transport (Cowen et al., 1993, 2000; Grioche et al., 2000). Apart from specific transport mechanisms, the present study demonstrates an overall link between larval vertical distributions and transport for multiple species. Species that moved inshore or remained on the shelf were found deeper in the water column than species that were exported from the shelf. Cowen et al. (1993) indicated that as larvae on the northeast U.S. shelf edge move deeper, they become more susceptible to onshore flows. Similarly, Cowen et al. (2000) argued that pomacentrid larvae are distributed at mid-depths off Barbados, and these mid-depth distributions resulted in larval retention

closer to the island. Peterson (1998) proposed that in upwelling systems, copepods can affect retention on the shelf through ontogenetic vertical migrations, whereby younger stages inhabit the upper offshore-flowing water and older stages inhabit the lower onshore-flowing water (see also Peterson et al., 1979). Similar models were developed by Pillar et al. (1989) and Barange and Pillar (1992) for euphausiids in the Benguela upwelling zone. Additionally, Batchelder et al. (2002) indicated that copepods can be retained nearshore in upwelling systems through diel vertical migrations between offshore-flowing surface waters and onshore-flowing bottom waters. From these studies and the results from the present study, a general hypothesis emerges that in many marine systems, fish larvae and zooplankton can affect onshore transport by moving deeper in the water column. Thus, similar to selective tidal stream transport whereby larvae use predictable tidal flows to either remain in estuaries or enter estuaries (Forward and Tankersley, 2001), general features in circulation may exist across physical oceanographic systems that allow larvae to influence their cross-shelf transport through basic changes in their vertical distribution.

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Appendix 1

Significant pairwise differences between the average larval vertical distributions of 10 species on the southeast United States continental shelf. A total of 187 comparisons were made and the 69 significant differences are listed below. Significant differences between average depth distributions were determined by using a test of independence with the cell values as average proportion of larvae at depth, averaged over a station occupation and weighted by the mean larval concentration at the station. A Bonferroni correction was applied to significance tests within each station occupation. The direction of significant differences (shallower [<], deeper [>], and different [<>]) was determined from the standardized residuals from the test of independence.

Year	Station	Species A		Species B
1986	Offshore	*Brevoortia tyrannus*	<	*Peprilus triacanthus*
1986	Offshore	*Brevoortia tyrannus*	<	*Paralichthys* spp.
1986	Offshore	*Brevoortia tyrannus*	<	*Leiostomus xanthurus*
1986	Offshore	*Brevoortia tyrannus*	<	*Etropus* spp.
1986	Offshore	*Brevoortia tyrannus*	<	*Etrumeus teres*
1986	Offshore	*Bothus* spp.	<	*Peprilus triacanthus*
1986	Offshore	*Bothus* spp.	<	*Paralichthys* spp.
1986	Offshore	*Bothus* spp.	<	*Etrumeus teres*
1986	Offshore	*Peprilus triacanthus*	>	*Leiostomus xanthurus*
1986	Offshore	*Peprilus triacanthus*	>	*Micropogonias undulatus*
1986	Offshore	*Peprilus triacanthus*	<>	*Etropus* spp.
1986	Offshore	*Peprilus triacanthus*	<>	*Etrumeus teres*
1986	Offshore	*Paralichthys* spp.	>	*Leiostomus xanthurus*
1986	Offshore	*Paralichthys* spp.	>	*Micropogonias undulatus*
1986	Offshore	*Paralichthys* spp.	<>	*Etropus* spp.
1986	Offshore	*Paralichthys* spp.	<>	*Etrumeus teres*
1986	Offshore	*Leiostomus xanthurus*	<	*Etropus* spp.
1986	Offshore	*Leiostomus xanthurus*	<	*Etrumeus teres*
1986	Inshore	*Brevoortia tyrannus*	<	*Peprilus triacanthus*
1986	Inshore	*Brevoortia tyrannus*	<	*Paralichthys* spp.
1986	Inshore	*Brevoortia tyrannus*	<	*Leiostomus xanthurus*
1986	Inshore	*Brevoortia tyrannus*	<	*Micropogonias undulatus*
1986	Inshore	*Brevoortia tyrannus*	<	*Etrumeus teres*
1986	Inshore	*Peprilus triacanthus*	>	*Paralichthys* spp.
1986	Inshore	*Paralichthys* spp.	<>	*Etropus* spp.
1989	Offshore	*Bothus* spp.	<	*Etropus* spp.
1989	Inshore	*Brevoortia tyrannus*	<	*Leiostomus xanthurus*
1989	Inshore	*Brevoortia tyrannus*	<	*Etropus* spp.
1989	Inshore	*Brevoortia tyrannus*	<	*Etrumeus teres*
1991	Offshore	*Brevoortia tyrannus*	<	*Bothus* spp.
1991	Offshore	*Brevoortia tyrannus*	<	*Peprilus triacanthus*
1991	Offshore	*Brevoortia tyrannus*	<	*Paralichthys* spp.
1991	Offshore	*Brevoortia tyrannus*	<	*Leiostomus xanthurus*
1991	Offshore	*Brevoortia tyrannus*	<	*Micropogonias undulatus*
1991	Offshore	*Brevoortia tyrannus*	<	*Etropus* spp.
1991	Offshore	*Brevoortia tyrannus*	<	*Etrumeus teres*
1991	Offshore	*Bothus* spp.	<	*Leiostomus xanthurus*
1991	Offshore	*Bothus* spp.	<	*Micropogonias undulatus*
1991	Offshore	*Bothus* spp.	<	*Etropus* spp.
1991	Offshore	*Bothus* spp.	<	*Etrumeus teres*
1991	Offshore	*Peprilus triacanthus*	<	*Leiostomus xanthurus*
1991	Offshore	*Peprilus triacanthus*	<	*Micropogonias undulatus*
1991	Offshore	*Peprilus triacanthus*	<	*Etrumeus teres*

continued

Appendix 1 (continued)

Year	Station	Species A		Species B
1991	Offshore	*Paralichthys* spp.	<	*Leiostomus xanthurus*
1991	Offshore	*Leiostomus xanthurus*	<>	*Etropus* spp.
1991	Offshore	*Leiostomus xanthurus*	<>	*Etrumeus teres*
1991	Offshore	*Etropus* spp.	<>	*Etrumeus teres*
1991	Inshore	*Brevoortia tyrannus*	<	*Bothus* spp.
1991	Inshore	*Brevoortia tyrannus*	<	*Paralichthys* spp.
1991	Inshore	*Brevoortia tyrannus*	<	*Leiostomus xanthurus*
1991	Inshore	*Brevoortia tyrannus*	<	*Micropogonias undulatus*
1991	Inshore	*Brevoortia tyrannus*	<	*Etropus* spp.
1991	Inshore	*Brevoortia tyrannus*	<	*Etrumeus teres*
1991	Inshore	*Bothus* spp.	<	*Peprilus triacanthus*
1991	Inshore	*Bothus* spp.	<	*Paralichthys* spp.
1991	Inshore	*Bothus* spp.	<	*Leiostomus xanthurus*
1991	Inshore	*Bothus* spp.	<	*Micropogonias undulatus*
1991	Inshore	*Bothus* spp.	<	*Etropus* spp.
1991	Inshore	*Bothus* spp.	<	*Etrumeus teres*
1991	Inshore	*Peprilus triacanthus*	<>	*Etropus* spp.
1991	Inshore	*Xyrichthys novacula*	<	*Micropogonias undulatus*
1991	Inshore	*Xyrichthys novacula*	<	*Etropus* spp.
1991	Inshore	*Paralichthys* spp.	<	*Micropogonias undulatus*
1991	Inshore	*Paralichthys* spp.	<	*Etropus* spp.
1991	Inshore	*Leiostomus xanthurus*	<	*Micropogonias undulatus*
1991	Inshore	*Leiostomus xanthurus*	<	*Etropus* spp.
1991	Inshore	*Micropogonias undulatus*	>	*Etropus* spp.
1991	Inshore	*Micropogonias undulatus*	>	*Etrumeus teres*
1991	Inshore	*Etropus* spp.	>	*Etrumeus teres*

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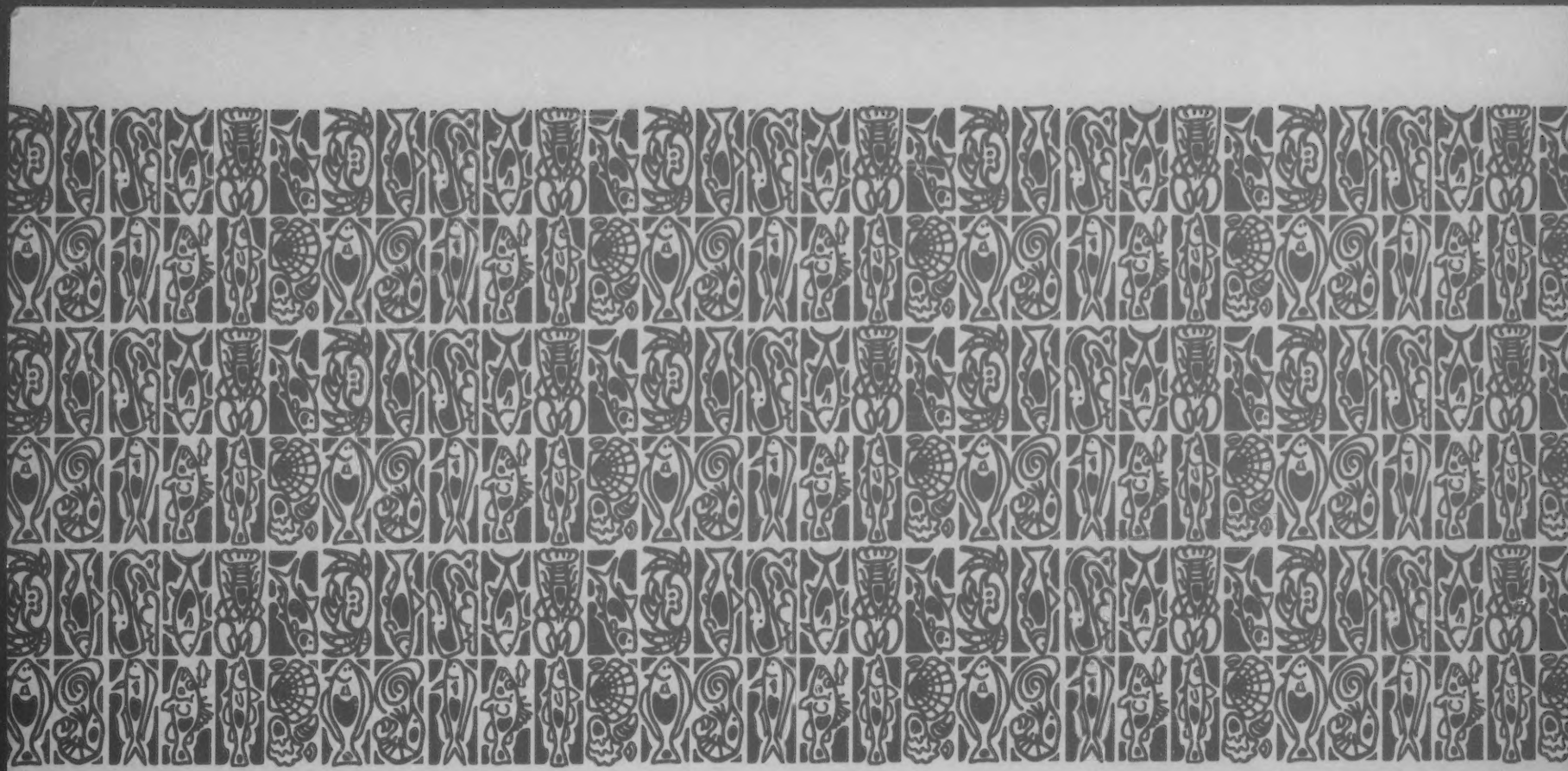

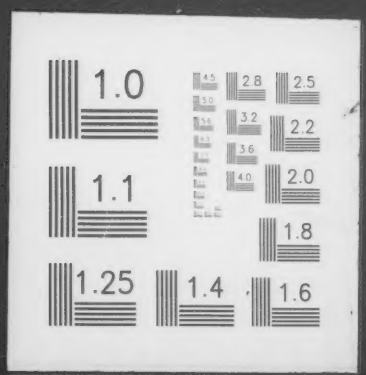
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